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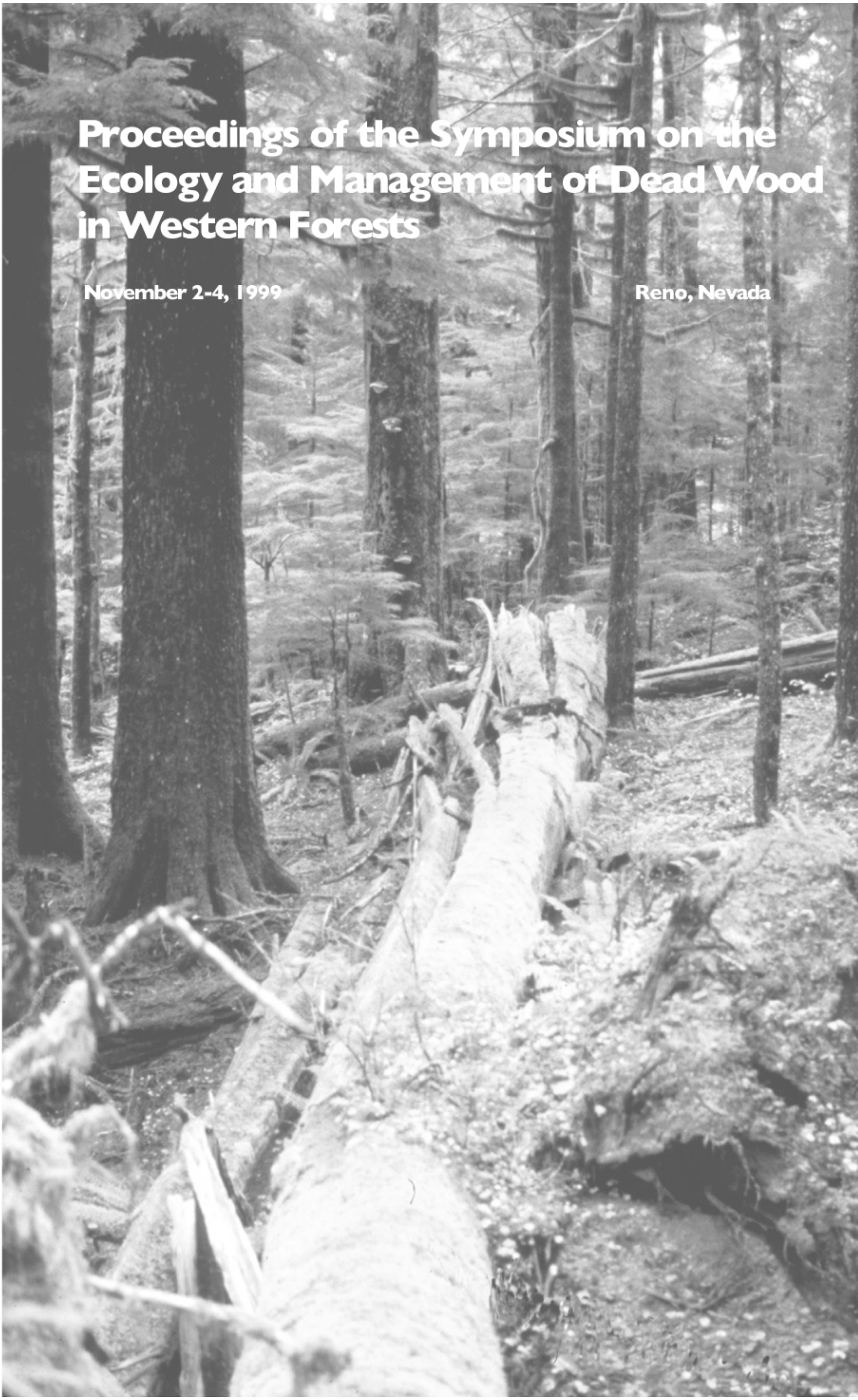
Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests

November 2-4, 1999

Reno, Nevada



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Contents

Importance of Dead and Downed Wood

Importance to Aquatic Systems

Importance to Invertebrates

Importance to Vertebrates

Importance to Soils and Other Forest Resources

Demographics and Dynamics of Dead Wood

Demographics and Dynamics in Coastal Mesic Forests

Demographics and Dynamics in the Cascades Forests

Demographics and Dynamics in Sierra Nevada Forests

Demographics and Dynamics in Rocky Mountain Forests

Management of Dead Wood

Perspectives and Approaches to Management

Symposium Synthesis

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Contents

Importance to Invertebrates 95

Importance to Vertebrates 169

Preface

Forest structure, especially snag and down log abundance and their spatial and temporal variation, can play a major role in the suitability of habitat for wildlife. Indeed, for some species, these attributes can be more influential than successional stage or topographic variables. Besides silviculture and timber harvest *per se*, other timberland management such as mechanical site preparation, broadcast burning, and fire prevention/suppression can directly or indirectly affect the quantity, quality, and dynamics of dead wood resources.

In 1997 and 1998, as a biologist for the California Department of Forestry and Fire Protection, I was asked to review and comment on the adequacy of proposed "Sustained Yield Plans" (SYP). Under the California Forest Practice Rules, owners of large areas of timberland were required to include in these plans a description of not only how they intended to generate maximum sustained production of high quality timber products but also how they would provide for fish, wildlife, and beneficial uses of water. These plans were intended to guide management of these lands with a 100-year planning horizon. Subsequent to the approval of an SYP, individual timber harvests tiered to them would likely undergo less environmental scrutiny and lighter analysis of potential cumulative impacts and mitigation. The combination of extensive areas and long time horizons of these proposals heightened the need for scientifically based review and modification, as necessary.

An early SYP submittal I reviewed from one of the large timberland owners, who exercised intensive management, prompted me to study proposed standards related to snags and down logs. Proposals for standards and the application of standards for regulations for forest management should be based on the best scientific information available, using professional judgment only to fill in holes. Additionally, under California law, standards based on the relationships of fish and wildlife species presence or abundance to management-sensitive variables carry more weight than do standards based on "reference conditions." I was familiar with many scientific studies on the values of snags (standing dead trees) to wildlife, especially primary and secondary cavity nesting birds. A number of suggested management recommendations and approaches had been well compiled in such places as Jack Ward Thomas' 1979 milestone *Wildlife Habitats in Managed Forests—the Blue Mountains of Oregon and Washington* and Davis and others' (1983) *Snag Habitat Management*. These documents provided good biological information and conceptual, logic-driven models that have formed the basis for subsequent modeling efforts. With the concern about the status of anadromous salmonids growing over the last decade or two, the knowledge base for the relationship of wood in streams with fish habitat value has been expanding and some guidelines have been developed. However, as far as I knew, the relationships and modeling of down logs on the forest floor were far less well considered. Wanting to provide a solid review and recommendation, I struggled with the paucity of region-specific information on the relationships of wildlife to all forms of dead wood, but felt very uncomfortable with the paucity of down log information. Thus these were some of the motivations behind the genesis of the idea for a symposium to synthesize past efforts and pull together current research on this important topic.

I spoke with several people about the idea, and everyone thought it would be a valuable contribution to both the resources involved as well as to the resource managers and scientists. Bill Laudenslayer of the USDA Forest Service was anxious to participate on the Technical Steering Committee and helped me identify others who might also have the expertise and connections to make it happen. The Steering Committee was formed, and consisted of Patrick Shea, Phillip Weatherspoon, Bill Laudenslayer, and Brett Harvey (Research Entomologist, Fire Ecologist, Wildlife Ecologist, and Fisheries Ecologist, respectively, Pacific Southwest Research Station [PSW], Forest Service); Gary Nakamura (Extension Forester, University of California Cooperative Extension); Dan Williams (Professor of Biology, California State University, Stanislaus); Lowell Diller (Biologist, Simpson Timber Company), and Don Owen and Brad Valentine (Entomologist and Biologist, respectively, California Department of Forestry and Fire Protection). This group met several times in Redding, California, to plan the symposium, despite the long distances necessary for some of us to travel in order to convene a meeting.

The desire of the Technical Steering Committee was to structure the symposium to promote understanding about the importance of dead wood resources in western forests, the processes that form and remove dead wood from forests, and application of management to the dead wood resource that could enable the development of scientifically-credible management recommendations. To that end, we grouped the sessions by these topics: the importance of dead wood to the forests' resources (aquatic systems, invertebrates, vertebrates, and soils); the dynamics and demography of dead wood in different forest systems; perspectives on dead wood management, and finally; guidelines for and ideas about dead wood management. To round out the information, we added preview and synthesis sessions.

The Steering Committee discussed several issues relative to the scope of the symposium. Which of the natural resources fields should we target for contributed papers and attendance, and would focusing on one field preclude participation by another? Would advertising the meeting as one directed at snags or wood in streams overwhelm and perhaps discourage submissions on down logs in terrestrial situations? Should we omit snags, since there is a more extensive history and probably current research focus on them, relative to logs? We decided to be broad-based, because we thought that focusing only on logs in the terrestrial ecosystem would result in too few submittals and perhaps miss the vital association between snags and logs. Another issue was the geographic scope. The entire Steering Committee resided in California, and one of the primary sponsoring institutions—the Western Section of The Wildlife Society—covers California and Nevada. However, we concluded that forest ecosystems across western North America were sufficiently similar that the concepts derived in one would be transferable to another; that the Steering Committee's personal contacts were wide enough that we could target invitations to provide valuable information attractive to a wide audience; and that especially with electronic communications a wide audience could be reached with symposium notices. The Steering Committee's decisions proved to be fruitful. The response to the "Call for Papers" underscored the timeliness of the topic for a symposium. The numerous submittals within the topic and geographic range necessitated concurrent sessions and interest was widespread with enquiries from Canada, Mexico, Australia, Europe, Russia, and Africa.

A very important foundation for developing a quality symposium is to invite selected speakers who can attract and energize the participants. Perhaps more important is that the invited speakers lend credibility to the symposium owing to their recognized expertise on the subject matter. The speakers we invited—Ann Bartuska, Robert Bilby, Evelyn Bull, Efren Cazares, Mark Harmon, Michael Haverty, Becki Heath, Paul Hennon, Lorin Hicks, Bruce Marcot, Robert Naiman, Catherine Parks, Christopher Rowney, Carl Skinner, Jack Ward Thomas, and Michael Wagner—fulfilled their roles well. Without their interest and participation, the symposium would have not been the high quality event that it turned out to be.

The Steering Committee could not accomplish all the work itself. We identified and invited other knowledgeable and capable people to act as Session Chairs. We asked the Session Chairs to not only introduce speakers and their presentations but also to run their sessions like tyrants keeping the talks on time and thus facilitating the concurrent session structure of the symposium. Far more than that, we asked Session Chairs to solicit papers for their sessions, and to review some of the manuscripts and make recommendations to the Editorial Committee regarding the quality of manuscripts for the proceedings. The Steering Committee would like to thank James Agee, Bruce Bingham, Lowell Diller, Carl Fiedler, Mark Harmon, Michael Haverty, Bruce Hostetler, Bill Laudenslayer, Thomas Lisle, Bruce Marcot, Don Own, Patrick Shea, Torolf Torgersen, Bradley Valentine, Phillip Weatherspoon, and Dan Williams for gladly assuming the extended range of Session Chair's chores.

The authors responded immediately and thoughtfully to the "Call for Papers" and followed well the manuscript guidelines, making the Editorial Committee's job that much easier. The Steering Committee placed another burden on authors that is not common in other symposia. Authors were required to have their manuscript "peer-reviewed" by two people knowledgeable in the field associated with their topic before submitting it to the Session Chairs or the Steering Committee. At least one of their reviewers had to be someone who was unrelated to their project. Finally, all technical manuscripts were reviewed by the Editorial Committee to meet publishing standards, and the PSW editorial staff provided style editing after the technical editing was completed. Technical manuscripts thus received at least three, and some received four, reviews prior to being included in the proceedings. Non-technical papers (literature reviews, perspectives, symposium introduction, and synthesis) did not undergo "peer review," but were reviewed editorially for style and content.

Bill Hull, then Executive Secretary for the Western Section of The Wildlife Society, relieved the Steering Committee of some of the logistical burden of staging a major event such as this. He negotiated and coordinated all the intricate details with the facility that hosted the conference. In addition, he managed the registration operations for the conference. He found the Atlantis Casino Resort in Reno, Nevada, to be a hospitable facility with which to work.

Four of the original Steering Committee members stayed on after the symposium to finish the task of publishing the proceedings. This "Editorial Committee"—Phillip Weatherspoon, Patrick Shea, Bradley Valentine, and Bill Laudenslayer—continued to meet and to communicate, to review manuscripts, and to prepare them for publishing. We soon realized that our group lacked the expertise to review hydrologic and aquatic manuscripts; thus, we invited Tom Lisle to participate on our Editorial Committee—a role that he graciously accepted. Bill Laudenslayer assumed the yeoman's job of chairing the Editorial Committee, one that we all wish to acknowledge.

Bradley E. Valentine, Technical Coordinator

Acknowledgments

The symposium would never have happened without the support of the organizations represented on the Steering Committee: Simpson Timber Company; California State University, Stanislaus; California Department of Forestry and Fire Protection; and the Pacific Southwest Research Station, USDA Forest Service. We also thank the Western Section of The Wildlife Society for assuming the up-front risk and providing the staffing support to make the "Symposium on the Ecology and Management of Dead Wood in Western Forests" an extraordinary success. Finally, without all of the participants, presenters, audience, and readers of these proceedings, there would not have been any reason to organize this symposium and prepare the proceedings.

We thank the symposium attendees, speakers and authors, and session chairs for their interest and contributions that provided the reason for publishing this volume. We greatly appreciate the work of Bill Hull for his considerable contributions to the arrangements and the operations of the symposium. We also thank all of the reviewers of the individual papers who contributed to and improved each paper. The formatting of manuscripts by Nydia Whimberly, Sandy Hicks, and Leticia Vidrio was essential to completing the proceedings, and we greatly appreciate their contributions. We also greatly appreciate the work of Martha Shibata, who designed the proceedings cover. Finally, we owe a great debt to Laurie Dunn, who edited every paper to ensure that they read smoothly and met the formatting standards, managed the work flow process, and prepared the final page layout of the manuscripts for the proceedings. Thanks to you all!

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Abstract

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Dead trees, both snags (standing dead trees) and logs (downed dead trees), are critical elements of healthy and productive forests. The "Symposium on the Ecology and Management of Dead Wood in Western Forests" was convened to bring together forest researchers and managers to share the current state of knowledge relative to the values and interactions of dead wood to and in a functioning forest. Topics covered include the value of dead wood organisms in both terrestrial and aquatic habitats, the dynamics of dead wood, and ecological, industrial, and State and Federal land management agency perspectives. This information is immensely valuable to researchers and managers working with or managing dead wood in a variety of ecosystems.

Retrieval Terms: cavity-dependent species, dead and down wood, dead wood distribution, dead wood value, debris flows, logs, snags, tree mortality

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Importance of Dead and Downed Wood

Dead Wood: From Forester's Bane to Environmental Boon[1]

Jack Ward Thomas[2]

Abstract

Forest managers are increasingly aware of the significance of Aldo Leopold's admonition that "to keep every cog and wheel is the first rule of intelligent tinkering." Dead wood, standing and down, is one of those "cogs and wheels." This was recognized in the 1970s and triggered additional research and evaluation of management action related to dead wood in managed forests. Much of this new information will be discussed at this conference. What will remain at the close is the essential need for synthesis of this new knowledge from research and management experience into a useable form for managers. This is the remaining challenge.

Introduction

When Patrick Shea approached me about giving this keynote address, I asked if he had thought about what comedian Jay Leno could do with a "government" conference on "dead wood." I accepted only after checking to see if the Office of Personnel Management was a co-sponsor. Then I began to consider why a retiree had been asked to deliver the keynote address and decided to quit thinking about such things. I remembered what my old friend and mentor Les Pengelly said when I congratulated him on a great keynote address at a conference on mule deer management: "Just remember what is happening when you are frequently selected to give keynote addresses. Your friends and colleagues remember you fondly, but know that you are really out of the game." Thank you for the honor and remembering me.

Dead Wood as the Bane of Forestry

There are a number of us in the room who can remember, in the early stages of our careers, when dead wood in any form was considered the bane of foresters who had been trained to focus on the most efficient commercial production of wood and wood fiber. Snags (standing dead trees) were considered a safety hazard to woodland workers and a potential source of spreading sparks that ignited spot fires. Down woody material was considered "fuel" that facilitated the spread of fire, a haven for vertebrate pests that hampered reforestation, and unsightly (Maser and others 1979).

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4 1999, Reno, Nevada.

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The Times They Are A'Changin'

Like the verse from the old Bob Dylan song, "The times they are a'changin'." At this conference, we are gathered to discuss the ecological role of dead wood in our dynamic search for means of attaining sustainable forest management.

Let me begin with a quote from Aldo Leopold (1953):

> The land is one organism. Its parts, like our own parts, compete with each other and cooperate with each other. The competitions are as much a part of the inner workings as the cooperations. You can regulate them cautiously but not abolish them…. If the biota, in the course of eons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first rule of intelligent tinkering (p. 146-147).

I often ponder why Aldo Leopold's admonition about keeping "cogs and wheels" is widely quoted and how often we are surprised at the consequences, both ecological and political, when it is ignored. By now, we should have learned that all the segments of a "naturally" functioning ecosystem play some role in that system whether or not we understand all the relationships. And we should have learned by now that biological systems are significantly simplified at some peril to the maintenance of that system.

System Simplification Implies Risk

Obviously, gross simplification of naturally occurring ecosystems has produced the means whereby dramatically increasing human populations could be supported. In some cases, such as in Western Europe, the U.S., and Canada, this has led to a lifestyle of the common people that would have been deemed impossible only one generation earlier. Today, however, experience is beginning to accumulate that such simplification may carry the seeds of diminution of productivity over the longer term.

The consideration of dead wood as one part of the essential functioning of forested ecosystems (including all of its component parts—biotic and abiotic) can be most instructive. We should keep in mind during these deliberations that dead wood is only one of many attributes of the forested ecosystems of the world. However, the discussion will undoubtedly elaborate Paul Ehrlich's corollary to Aldo Leopold's admonition about saving cogs and wheels. It is the "why" to the first rule of intelligent tinkering—"all things are connected and there are consequences to all manipulations of biological systems" (Ehrlich and Roughgarden 1987).

Recognizing the Importance of Dead Wood: Better Late Than Never

In retrospect, it is amazing that forest managers did not realize that dead wood was a critical habitat component—for vertebrate and invertebrate wildlife and for the forest itself. Elton (1966) succinctly described the role of dead wood as a critical habitat component:

> When one walks through the rather dull and tidy woodlands…that result from modern forestry practices, it is difficult to believe that dying and dead wood provides one of the two or three greatest resources for

> animal species in a natural forest, and that if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna (p. 279).

By using the example of Wyndam Wood in England, Elton (1966) described the number of species that might be related to dead wood as habitat: "Indexes of the Ecological Survey contain 456 species of animals (including invertebrates)… living in wood or under bark where decay has begun or already gone far. Another 518 species are known to occur in this habitat elsewhere in Britain…." (p. 279).

By the 1970s, researchers and forest managers were becoming increasingly aware of the role of dead wood in the ecology of the managed forest. The important implications of decomposing woody debris in mineral cycling, nutrient immobilization (Fogel and Cromack 1977, MacMillan and others 1977), and nitrogen fixation (Cornaby and Waide 1973) had been put forward. Logs were recognized as frequently serving as substrates for fungal hyphae, rhizomorphs, and sporocarps (Ausmus and others 1975, Cromack and others 1975). Harvey and others (1976) had demonstrated the role of decaying logs as sites for colonization of ectomychorrhizal fungi that aided in the survival of several species of trees. Mychorrhizal fungi had been shown to aid processes of nitrogen fixation (MacMillan and others 1977). Cromack and others (1975), Maser and others (1978), Miller and Halls (1969), and Trappe and Maser (1976) had identified fungi associated with dead wood as an important food source for both vertebrate and invertebrate wildlife. Earlier, Graham (1925), Kimmey and Furniss (1943), and Savely (1939) had noted that decaying logs provided varying attributes of wildlife habitat, depending on the state of decay.

Researchers, most of whom were associated with the USDA Forest Service research unit at La Grande, Oregon, began multi-disciplinary cooperative studies in the late 1970s to further expand knowledge about mortality factors associated with the western spruce budworm *(Choristoneura occidentalis)* (Campbell and others 1983, Campbell and Torgerson 1982, Torgerson and Campbell 1982). They identified and quantified the major effects of insectivorous birds (most of whom were secondary cavity nesters) and foliage-foraging predaceous ants as regulators in the dynamics of low-level budworm populations. There were 13 species of ants (11 of which were associated with dead wood) identified as predators on the budworm (Genus *Camponotus* and *Formica*) (Torgerson and others 1990).

Bull and others (1992) determined that a major portion of the diet of pileated woodpeckers *(Dryocopus pileatus)* were the same species that were major predators on spruce budworm. Torgerson and Bull (1995) collaborated in the characterization of logs that were habitat for ants and used by pileated woodpeckers for foraging.

They found that budworm outbreaks occur about every 40 years (Swetnam and others 1995). After trees are killed, some become snag-habitat for woodpeckers, secondary cavity nesting insectivorous birds, and ant predators of the budworm. The snags become down logs, which then become the home for colonies of ants and forage for woodpeckers. Ants and birds are dominant regulatory forces on budworm populations at low population levels. Decaying wood simultaneously plays a role in nutrient cycling. Outbreaks eventually occur, tree mortality results, and the cycle begins anew (Torgerson, pers. comm.).

Everything Is Connected to Everything Else

At this meeting, we will discuss the role of dead wood in forested ecosystems, including its role in associated aquatic systems. We will examine at least some of the connections between dead wood and "everything else" in the healthy forest, and this is only the beginning of knowledge. As Aldo Leopold (1953) stated: "The outstanding scientific discovery of the twentieth century is… the complexity of the land organism. Only those who know the most about it can appreciate how little we know about it…" (p. 146).

Yet, it is clear that there can be no respite from our tinkering with natural systems. As with all our fellow creatures, human populations must exploit the environment in order to live. There is no question about that. The question, then, becomes one of how such exploitation occurs. The challenge of the new millenium for natural resource managers is the question of how we can exploit our environment and maintain its productivity and health (defined as the capacity for renewal)—not only for the short term but also for the centuries. That is what the buzzwords such as "sustainability," "ecosystem management," and "forest health" mean. At least for the foreseeable future, this will be a challenge because of the increasing human population.

The Growing Need for Synthesis and Re-synthesis

In this conference, we will address a small piece of the concerns of how forest managers can combine the objective of meeting people's needs and, simultaneously, maintain forest health. The journey of learning and understanding more and adjusting management will be a continual feedback loop that will require constant adjustments in management. This is inevitable and should be accepted as part of routine business.

I predict there will be, at the end of our deliberations, a sense of confusion among the managers in attendance about the information and insights presented here. Managers will probably be overwhelmed with the various bits of new information, insights into the role of dead wood in forested ecosystems, and the various suggestions for the management of the dead wood component. That inevitable confusion will require synthesis of the myriad pieces of information into some useful, and defensible, form for the use of managers. And, who will do that chore? It seems likely, if past is indeed prologue, that the essential synthesis will be "blowing in the wind," as the individual presenters retreat into their specialized niches in research organizations.

Synthesis: It Has Been Done Before

It does not have to turn out that way. I hope that before this conference ends an *ad hoc* team has been formed that is pledged to the synthesis of the material presented here, and material that can be found elsewhere, into a useful treatise on the subject of the role and management of dead wood in managed forests. This can be done. It has been done before, beginning with some chapters entitled "Snags" (Thomas and others 1979) and "Dead and Down Woody Material" (Maser and others 1979) in the document *Wildlife Habitats in Managed Forests—The Blue Mountains of Oregon and Washington* (Thomas 1979).

Synthesis: Not for the Faint of Heart

It took nerve to go forward with the synthesis of the extant information (which was sparse compared to what will be presented at this conference), make informed "guesses" when detailed understanding based on "hard data" was lacking, and then make suggestions to management. Frankly, it will take nerve to take the next step. Synthesis and management guides are not for the faint of heart. In this action lies the bridge from creation of knowledge and pontification to responsibility.

There was some applause and some criticism. One critic criticized us in a meeting with the accusation that we had "guessed" at some critical points. I conceded that he was correct, but that we offered no apologies. The "guesses" (we preferred the descriptive term of "informed opinion") were clearly identified as such. But, if nothing else, we had put forward a number of hypotheses that he and a number of other researchers—including ourselves—were chasing. In the meantime, we had certainly brought attention to the need to consider dead wood in forest management. Changes could be made in response to better research-based data when such was available. I am certain that we will see a great deal of that improved knowledge at this conference.

We considered that 71 species of birds and 51 mammals (122 out of 378 vertebrate species in the Blue Mountains—32 percent) depended to some degree on snags as a habitat component. When we further considered that snags were becoming ever more scarce under the forest management regimes in place, it was clear that there was a problem developing (Thomas and others 1979). That problem could take the form of an impending collision with the Endangered Species Act of 1973. Or, more likely, there was a problem that was related to the purpose of that Act ("to provide a means whereby the ecosystems upon which endangered and threatened species depend may be conserved" [Endangered Species Act of 1973, Sec. 2 (b) (1)]).

This was likewise true of down woody material. We believed that 5 amphibians, 9 reptiles, 116 birds, and 49 mammals (179 out of 378 vertebrate species—47 percent) made some use of logs and other down woody materials (Maser and others 1979).

Synthesis: The Two Choices Are "Too Soon" and "Too Late"

We were criticized by some of our colleagues who maintained that we were "premature" in our findings and in our recommendations for management. We looked those colleagues squarely in the eye and announced that, in our minds, we had two choices—"too soon" or "too late." We opted for the former and challenged managers to test the hypotheses and develop a deeper understanding of the role of dead wood in the forests. Our view was summed up in the following statement from Thomas (1979):

> Perhaps the greatest challenge that faces professionals engaged in forest research and management is the organization of knowledge and insights into forms that can be readily applied. To say we don't know enough is to take refuge behind a half-truth and ignore the fact that decisions will be made regardless of the amount of information available. In my opinion it is far better to examine available knowledge, combine it

with expert opinion on how the system operates, and make predictions about the consequences of alternative management actions.

Synthesis? Just Do It

This is the challenge I present to you today. Do not walk away from this conference content with a publication of dozens of additional pieces of disjunct information and recommendations. That leaves the job half-done. Surely, in this audience is a team just waiting to be formed that can and will produce a summary treatise on the role of dead wood in managed forests that will help guide managers as they struggle toward sustainable forestry. If not, I suggest that we may just have wasted our time and produced one more publication to add to a thousand others on library shelves where it will reside until someone seeks synthesis. Through experience, I have found that pontification is far less risky, and far easier, than assumption of responsibility. But, in the exercise of responsibility lies the ability to make change and be accountable. Take the responsibility.

It has been done before, 20 years ago, with much less information than exists today, and it made a difference. This conference will significantly reinforce the base of information and understanding.

Now is the time. The need is apparent. There is more and better information than ever before. All that is required is courage, some "street smarts," the will, hard work, credibility, and the guts to put reputations on the line. My final plea is do it, just do it.

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Decaying Wood: An Overview of Its Status and Ecology in the United Kingdom and Continental Europe[1]

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Abstract

Decaying wood habitats are rare in Europe because of centuries of forestry and agricultural practices. Where there has been continuous woodland cover and within it an unbroken presence of old trees, the decaying wood communities are exceptional. The main woodland management systems operating in Europe are explained and how they influence the decaying wood component and associated wildlife. Priorities for conservation in a European context are outlined and selections of important old-growth sites are provided.

Introduction

Dead, or perhaps more accurately, decaying wood and much of the wildlife associated with it has become very rare in Europe. Any form of agriculture or forestry diverts natural resources from wildlife towards human activity (Fry and Lonsdale 1991), and our history is one in which timber and woody material have been removed from our woodlands. In traditional systems man would have utilized nearly every piece of wood. Today, dead trees are still cleared to make way for new tree crops; sanitation felling and burning is still practiced to protect lowland broadleaved forestry crops from a misguided perception of infection (Winter 1993); and a tidiness mentality overrides all. Mechanized operations encourage more intensive exploitation of timber produce and drive earlier and earlier returns on capital expenditure, reducing the age of standing tree crops and at the same time increasing the scope of sanitation and tidiness activities.

Intensive land use over the centuries and especially in the past 50 years has led to massive loss of a whole range of semi-natural habitats, and those that remain have become ever more isolated. Only a maximum of 10 percent of the land surface of most of Europe today remains in some more or less "semi-natural" condition (Speight 1987). In the United Kingdom (UK) nearly 50 percent of ancient woodland has been lost since 1947 (Fry and Lonsdale 1991). Between 1979 and 1990 there was a 14 percent loss of vegetation species richness in woodland—the highest for any

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habitat in the UK (Department of the Environment 1994). Because dead wood within existing semi-natural woodland is poorly represented, relic decaying wood communities have become more isolated than most.

Because the situation became more alarming, the Council of Europe (1988) adopted a recommendation on the protection of saproxylic organisms and their biotopes. This highlights that Europe is beginning to understand the importance of the decaying wood ecosystem. Since the 1990s, there has been a gradual change and the protection of decaying wood habitat is now cited as an environmental concern in forestry policy and procedures in many European countries.

Ancient Woodland

Ancient woodland is woodland that has existed since at least the 16th century on the same site, although it may have been managed throughout the centuries. Less than 2 percent of the land area of Britain is ancient woodland and mainly comprises small areas separated from each other by intensively managed landscapes; more than 8 out of 10 woodlands are less than 20 ha (50 acres). In many of these ancient woods there has always been woodland cover of one type or another that retains a continuity of habitat structure similar to the wild wood or virgin forest, which developed after the last ice age around 7,500 years ago. This continuity of woodland cover provides a habitat and biodiversity that is irreplaceable. However, in many cases the woodland often comprises young stands of trees. In ancient woods containing old trees and where there has been a continuous presence of old trees on the site, i.e., old-growth woodland, additional assemblages of rare wood-decaying species can be found.

Wood Pasture

Wood pastures are extensively grazed, open-structured woodlands that allow the regeneration of open grown trees, especially shade intolerant species. Trees in these open conditions have a much shorter, stockier stature as they achieve a full canopy without needing great height. As they age they become hollow, and the canopy may reduce further. Often there has been a tradition of pollarding the trees—regular cutting of the trees at head height or higher on rotation—for a renewable source of wood that has been very beneficial for the creation of decaying heartwood. The old trees are very important for decaying wood communities. Wood pastures are very vulnerable to intensification of use—changes that increase productivity of grass and overgrazing, which results in trees that are severely affected by high chemical inputs from fertilizers, pesticides and animal drugs, compaction, and water logging (Alexander and others 1996, Read 2000). This more open type of habitat is also particularly vulnerable to external influences, such as spray drift and air pollution from surrounding intensive grazing and arable production systems. British wood pastures and parkland are more common than in mainland northwest Europe probably because there has been a continuity of land ownership by the aristocracy who used wood pasture and parkland for deer hunting.

Coppice Woodland

By the Middle Ages, the typical management for coppice resulted in widely spaced trees that grew to maturity. Because of frequent harvest on short rotations of the wood resource through the centuries, this woodland is most likely to have low quantities and a limited dead and decaying wood structure. However, old coppice stools, which survive and increase in size and age through many harvesting cycles, provide continuity of dead wood habitat. The old stools are known to be especially valuable for saproxylic hoverflies and other Diptera that favor decay in moist situations.

High Forest

By 1980, 75 percent of UK broadleaved woodland was managed as high forest (Hart 1994). Although accumulation of decaying wood in unmanaged woodland may amount to 50-200 cu m per hectare, in conventional high forest managed systems it may well be as low as 1-5 cu m per ha, and the variety of the dead wood resource tends to be much diminished by such management (Ferris-Kaan and others 1993). Many European countries are increasing the areas of minimum intervention woodland—that are largely untouched by people except to combat unwanted human influences. This should allow decaying wood levels to rise within them once again.

Wet Woodland

Wet woodland, such as Atlantic or oceanic woodland—which is characterized by cool, wet climate with few temperature extremes or woodland with wet features such as springs, streams, or rivers—can be especially important. This habitat supports humidity-demanding dead and decaying wood species, which are now very rare in Europe, and many of those that remain have been badly degraded by overgrazing (Hodgetts 1996).

Comparisons with Continental Europe

In much of continental Europe, forests generally are young high forest stands of trees, as wood is still a major source of fuel for local communities; whereas in Britain, coal, natural gas, and nuclear fuels have provided significant alternatives for centuries. The UK has more old trees in ancient woodland, wood pasture sites, and traditional agricultural landscapes than most other northern European countries (Green 1994). These ancient sites with existing old trees and shrubs contain characteristic dead and decaying wood communities, especially fungi, lichens and invertebrates. Because some of the trees can be more than 1,000 years old and many more than 500 years old, only a small number of generations have spanned the period between the last Ice Age and today (Key, pers. comm.).

Decaying Wood and Its Wildlife

Dead wood has a limited existence: it decays and is ultimately recycled. Conservation of wood decay communities requires conservation of a diverse age structure of living trees to senility and death because the living tissues generate the wood, which will ultimately decay. A continuity of different wood decay habitats in individual trees, above- and belowground and a variety of standing and fallen wood in different environments in woodland is therefore necessary to ensure sustainable wood decay communities.

The most important wood decay resources are large, old, standing, living and dying trees that develop columns of decay in the dead heartwood or center of the tree. Fungi are fundamental to the decay process.

Fungi

"A tree (or woodland) without fungi is like a stage without actors. For, throughout its life a tree generates a mobile wooden framework upon and within which literally countless fungi enact diverse ecological roles. Whereas some fungi bring resources to the tree others degrade and recycle its products" (Rayner 1996).

In Europe, "fungi do not figure in the usual brief for wildlife or habitat conservation. No voice has been raised on their behalf. They, however,… stoke the power plant of the forest. The more substantial the vegetation, the greater the variety of fungi for its degradation" (Corner 1994).

In the UK the role and importance of fungi in the wood decay system and in habitats generally is only starting to be recognized. Despite their importance at the center of woodland ecology, they have been largely overlooked and dismissed. Very old trees are exceptionally valuable for fungi, and the fact that the trees have reached an advanced age at all may be largely due to their relationship with fungi.

White rotted heartwood and brown rotted heartwood are produced as a result of non-pathogenic fungi digesting the principle wood components–lignin or cellulose, respectively. It is this decay process that creates the succession of decaying wood habitats that other species can exploit. Various other fungi can decompose or naturally prune the aerial parts of the trees in site; however, frequently different soil-inhabiting, decomposition fungi colonize the wood when it falls to the ground. Belowground fungi are also present colonizing roots. Finally, the fungal mycelium or fruit bodies themselves can provide specialist habitats for another community of invertebrates. The natural process of breakdown of dead wood releases valuable nutrients, which then can be recycled often via mycorrhizal fungi to living parts of the tree.

Invertebrates

About 6 percent of the entire British invertebrate fauna breed in or feed exclusively on other species that breed in decaying wood (Alexander 1999). This translates into 1,700 species with different lifestyles, since each species has very particular requirements. Very few invertebrates possess the necessary gut enzymes to break down the principle components of wood—cellulose and lignin—so most rely on fungi and other micro-organisms to convert them into something more edible.

In both brown and white heart rot, the end product is black wood mulch, which accumulates in the bottom of the hollow trunk as the fungi work into the upper trunk and main boughs. Fifteen percent of Britain's rarest insects, listed in the *British Red Data Book* (Shirt 1987), develop in this medium of relatively constant temperature and humidity, protected from the outside world by the surrounding living trunk tissues—for example, the click beetles *Lacon querceus* and *Ampedus cardinalis*. Specialist invertebrates also exploit the communities in and on the bark, including the epiphytic lichens.

Lichens

The most well-known epiphytic lower plant community is the *Lobarion pulmonariae*. *Lobarion*-rich parkland, with its well spaced ancient trees and a continuity of old trees, is of extreme importance for these and other lower plants; they are quantitatively richer and qualitatively different, holding a considerable number of epiphytic species confined, or nearly so, to such habitats (Rose 1991). Although lichens may not be confined to the largest or oldest trees, the presence of ancient trees in the area is the feature most strongly associated with lichen-rich stands. The *Lobarion pulmonariae* would be the climax epiphytic community in lowland Europe, but it has largely disappeared because of tree felling and pollution (Hodgetts 1996).

Lichens are key indicator species, demonstrating continuity of old trees on a site that is also well suited for fungi and saproxylic invertebrates.

Mammals and Birds

Some of the UK's most charismatic animals—woodpeckers, owls and bats—are associated with decaying wood habitat. These animals find opportunities for cavity nest sites in the dead wood and a wealth of invertebrate life in the food chain. Many are under severe threat in Western Europe—such as the Eurasian flying squirrel *(Pteromys volans)* and white backed woodpecker *(Dendrocopos leucotos)* (Spiridinov and Virkkala 1997)—due to the intensification of forestry practices and the effectiveness of sanitation felling.

Identifying Good Dead Wood Habitat: Demonstrating Continuity

Indexes of ecological continuity have been developed for lichens (Rose 1976) and saproxylic beetle fauna (Alexander 1988, Fowles and others 1999). Fungi representative of late stage successional habitats can provide further examples, although no index has yet been developed.

These indexes demonstrate that our priority is to perpetuate the continuity of wood decay habitats comprising old trees (both living and dead standing trees) on primary or ancient woodland sites.

Management for Decaying Wood in Europe

The wildwood of lowland Europe, in which wood-decaying communities were more frequent than today, comprised a mosaic of open sunlit glades, dappled by different densities of tree cover and dense high forest. It seems likely that there was a high proportion of woodland glades comprising low tree cover and dappled shade over extensive areas (Vera 1998). The glades would have been created initially by the role of fungi (Green 1996), sometimes in association with phytophagous insects and perhaps enlarged by other forces of wind, snow, fire, and erosion (Peterken 1996). However, in the UK the influence of fire and erosion is negligible (Rackham 1986). Once created they would have been kept open by browsing animals, many of which have long since disappeared from our woodlands (Dobson and Crawley 1994).

The priority in Europe is to identify and select areas of ancient old-growth or relic forest (Harding and Alexander 1994) and then maintain and perpetuate the continuity of old trees present on them. To perpetuate wood pastures, it is necessary to retain the remaining trees as long as possible, minimize damaging activities in their vicinity—for example, deep ploughing under the canopy of the trees—and promote the establishment of new stands of open-grown trees adjacent to existing stands or in close proximity (Alexander and others 1996).

It is also necessary to protect and enhance decaying wood in our semi-natural high forests and coppice woodlands by retaining far more variety and quantity of decaying wood habitats and especially to retain far more standing decaying trees of all ages. On these sites all fallen dead wood needs to be retained and "tidiness" discouraged. Equally as important is to ensure a sustainable provision of all types of decaying wood through the next millennium by retaining enough trees in each stand to become the decaying wood of the future.

The worst of all possible management scenarios is to burn the decaying wood (Green 1994, 1996). Along the Atlantic coast of northwest Europe, fire is not a natural part of the ecosystem of broadleaved woodlands. As decaying wood habitat is recycled by a succession of specialized species within the community, fire would seriously compromise natural processes.

Climate change and the isolation of habitats by intensification of land use will continue to have marked impacts on islands of biodiversity unless species populations have opportunities to develop and expand. Although there is all too little knowledge of the rate with which communities can expand and recover given suitable habitat directly connected or nearby to it, it is clearly a priority to identify the remaining vestiges of habitat that have a well differentiated fauna or flora of saproxylic organisms; manage them effectively; and buffer, extend, and ultimately work towards connectivity between them.

A Selection of the Most Important Decaying Wood Sites in Europe

- The New Forest—A remarkable area of wood pasture and the largest of its type in southern England.
- The North Cotswolds—A large area of traditional agricultural landscape with ash *(Fraxinus excelsior)* pollards in southern England. This area is remarkable for its richness of saproxylic fungi and invertebrates that is only slowly being recognized.
- The Lake District—An extensive landscape of pollard trees with exceptional epiphytic communities in northern England.
- Windsor Great Park—A high number of very large, old oak *(Quercus robur)* trees near London in southern England, some of which are over 1,000 years old, in a variety of environments from minimum intervention high forest, wood pasture and parkland, and intensive arable cultivation. This is perhaps the largest concentration of very old oak trees in the world in association with one of the highest indexes of continuity of saproxylic beetles and fungi in the UK.

- Fontainbleau Forest—Small areas of minimum intervention woodland in the midst of a large commercial and recreation forest by European standards, located southeast of Paris, France.
- Bialowieza National Park—The largest area of minimum intervention forest in Europe, 10,502 ha with some remnant old growth areas, located in eastern Poland.
- Island of Vilm—Former pasture woodland with no clearcutting since the 16th century. Nature reserve with old oak *(Quercus robur)* and beech *(Fagus sylvatica)* trees, located near the island of Ruegen, northeastern Germany.
- Bjärka-Säby—Larger oak *(Quercus robur)* woodland meadows now pastured by cattle, located South of Linköping, southeastern Sweden.

Glossary

Ancient woodland: Woodland that has existed continuously on the site since AD 1600 and has been cut only for under wood or timber production.

Semi-natural ancient woodland: Stands of ancient woodland comprised of mainly native species growing where their presence is apparently natural and not obviously planted.

Ancient replanted woodland: Ancient woodland sites with obviously planted woodland of a broadleaved, mixed or coniferous type.

Old-growth forest: [UK] Stands with more than 200 years' growth (Peterken 1996). Rose (1992) stresses the importance of continuity of trees older than 200 years.

Wood pastures and parkland: Historic land management systems that represent vegetation structure rather than a plant community and increasingly thought to mimic the structure of the natural forest before human activity. Typically this structure consists of large open-grown or high forest trees (often pollards) at various densities, in a matrix of grazed grassland, heath land and/or woodland floras.

Coppice: Trees cut regularly near the ground usually in rotation to produce a supply of small wood of small diameter for poles, stakes, and firewood. Usually grown with scattered trees allowed to grow to maturity without being cut back.

Pollards: Trees cut regularly at 2.5-4.0 m above ground level. At this point new shoots grow to provide a supply of small wood. The advantage of pollarding is that the land under the trees can be used at the same time as pasture for animals or stock without the danger of the animals eating the new shoots.

Native species: Trees and shrubs that colonized Britain unaided by human activity before the land bridge with mainland Europe was broken.

Exotic species: Trees and shrubs introduced into the UK by human activity in increasing numbers after 1600.

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Importance to Aquatic Systems

Influence of Bank Afforestation and Snag Angle-of-fall on Riparian Large Woody Debris Recruitment[1]

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Abstract

A riparian large woody debris (LWD) recruitment simulator (Coarse Woody Debris [CWD]) was used to test the impact of bank afforestation and snag fall direction on delivery trends. Combining all cumulative LWD recruitment across bank afforestation levels averaged 77.1 cubic meters per 100 meter reach (both banks forested) compared to 49.3 cubic meters per 100 meter reach (one side timbered). Both bank afforestation and snag fall patterns generated significant differences in riparian LWD delivery, but there was no noticeable interaction. Scenarios with only one bank forested delivered 15 to 50 percent less LWD than their two bank counterparts. Snag fall patterns also produced statistically different LWD recruitment, with some registering only 35 to 52 percent of the most productive fall patterns. These results suggest testing the assumptions of random snag fall from two forested banks before modeling riparian LWD recruitment.

Introduction

Large woody debris (LWD) recruitment is critical to healthy riparian ecosystems (Bisson and others 1987, Dolloff 1994, Kershner 1997), making its recovery a primary goal of streamside management (Berg 1995, Kershner 1997). Surprisingly little work has been attempted on long-term recruitment dynamics, as research has concentrated on the quantification of riparian LWD and its ecological role. However, a growing interest in computer modeling of riparian LWD recruitment has prompted the development of some simulators in recent years (e.g., Bragg and others 2000, Murphy and Koski 1989, Rainville and others 1985, Van Sickle and Gregory 1990).

While creating a new riparian LWD recruitment model, we became concerned about some traditional assumptions. For instance, most efforts have presumed that both banks are equally forested. Although this may be true in mesic regions, some semi-arid areas have limited forest on some banks. Modelers have also assumed random snag fall without testing this premise. Random tree fall patterns can occur when failure is not influenced by either disturbances or geomorphology (Maser and Trappe 1984, Robison and Beschta 1990, Van Sickle and Gregory 1990). Although most riparian LWD simulations have applied this pattern, other distinct

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configurations are possible (Alexander and Buell 1955, Bragg and others 2000, Grizzel and Wolff 1998, Schmid and others 1985, Veblen 1986). Another biasing factor, tree lean, plays only a limited role in riparian LWD delivery (Hairston-Strang and Adams 1998). We decided to test the influence of different bank afforestation and angle-of-snag-fall patterns on riparian LWD delivery to the stream using computer simulation, which we hoped would improve the long-term prediction of riparian LWD recruitment.

Methods

Project Design and Assumptions

The riparian LWD recruitment simulator Coarse Woody Debris (CWD, version 1.4) was used to predict bankfull channel delivery. CWD is a post-processor to the Forest Vegetation Simulator (FVS) (Wykoff and others 1982). We will only briefly describe the most salient features of the models' interplay (Bragg and others 2000). FVS establishes, grows, and kills all simulated trees, while CWD drives LWD formation and channel recruitment. CWD takes dead trees, places them within the riparian zone, selects an angle-of-fall from a predetermined distribution, fells and breaks the snag, and assigns which pieces are recruited to the channel. Both disturbance-related and self-thinning mortality can be emulated (Bragg 2000). CWD randomly assigns tree locations in relation to the channel. Because the angle-of-fall pattern set by the user is fixed for the whole riparian forest, biased fall directions should be carefully designed to ensure consistency with local conditions. Depending on the need, CWD allocated the trees to one or two banks. This effort assumed LWD was greater than 10 centimeters in diameter and more than 1 meter long and was "recruited" to the bankfull channel if it extended at least 1 meter into this zone.

Modeled Stream Description

Dry Lake Creek, a second order stream about 60 km northeast of Jackson, Wyoming, on the Bridger-Teton National Forest, was exclusively used for these simulations. Along the sampled reach, Dry Lake Creek had a mean bankfull width of 5.5 meters, an average gradient of 3.5 percent, a mean elevation of 2,565 meters, and drained an upstream basin of 1,033 hectares (Bragg and others 2000). Riparian LWD volumes within this reach of Dry Lake Creek averaged 8.6 cubic meters per 100 meter (Bragg and others 2000). The predominantly Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forests along Dry Lake Creek averaged approximately 33 square meters per hectare of live basal area. Both banks along this particular reach were wooded, but for demonstration purposes, half of the simulations considered only one side was forested. A bankfull width of 5.5 meters and a streamside forest depth of 38 meters for each bank were also assumed. All simulations covered 300 years.

Statistical Design and Analysis

In this study, we tested five different snag fall patterns: (1) random (RND); (2) the tri-modal CWD default (DEF); (3) snags falling primarily towards the channel (TWRD); (4) a fall pattern quartering towards the channel (QRT); and (5) snag failure largely paralleling the channel (PRL) under two bank afforestation conditions (one [O] or both [B] forested) *(table 1)*.

Table 1—*Treatment codes, descriptions, and predicted riparian LWD recruitment by bank afforestation and snag fall pattern.*

Treatment code	Description	Cumulative volume	Standard deviation
		---- m^3 per 100 m reach ----	
2 banks forested			
BRND	Random pattern	79.7	3.74
BDEF	Tri-modal (CWD default) pattern	78.4	5.18
BTWRD	Fall direction towards the channel	90.7	6.87
BQRT	Fall direction quartering towards channel	77.6	5.44
BPRL	Fall direction parallel to the channel	59.0	2.85
Pooled	Average of all 2 bank treatments	77.1	11.41
1 bank forested			
ORND	Random pattern	39.9	3.80
ODEF	Tri-modal (CWD default) pattern	38.4	2.60
OTWRD	Fall direction towards the channel	76.6	2.00
OQRT	Fall direction quartering towards channel	64.0	4.59
OPRL	Fall direction parallel to the channel	27.5	2.16
Pooled	Average of all 1 bank treatments	49.3	20.27

Because of the stochasticity in some CWD subroutines, 10 replicates were run for each snag fall pattern. Total LWD recruitment (in cubic meters per 100 meter reach) over the simulation period was compared to determine the cumulative significance of bank afforestation and snag fall patterns. Because of untransformable heterogeneity of variance and non-normal data distributions, the nonparametric two-factor extension of the Kruskal-Wallis (K-W) analysis of variance test and a multiple comparison using rank scores were used to identify treatment effects (Zar 1984).

Results

Both bank afforestation and snag fall direction significantly ($P < 0.05$) affected cumulative LWD recruitment to Dry Lake Creek, but there was no significant interaction between the two *(table 1)*. Recruitment was always lower from streams with one forested bank: when averaged across snag fall patterns, having both banks forested delivered 77.1 cubic meters per 100 meter reach (standard deviation [SD] = 11.41), while one forested bank treatments averaged 49.3 cubic meters per 100 meter reach (SD = 20.27).

With only one bank forested, random (ORND), default (ODEF), and OPRL snag failure patterns yielded almost 50 percent less LWD recruitment than the same patterns (BRND, BDEF, and BPRL) when both banks were forested. Of these treatments, only the BPRL versus OPRL comparison proved statistically insignificant. OTWRD and OQRT declined only 15 to 20 percent from BTWRD and BQRT. However, consistently lower LWD delivery from only one forested bank resulted in the rejection of the null hypothesis of no effect of bank afforestation.

The tree fall pattern predominantly towards the channel (TWRD) produced the most LWD recruitment (regardless of bank afforestation), while the patterns paralleling the channel (PRL) yielded the least *(table 1).* Even though BTWRD did not noticeably differ from BQRT, BDEF, and BRND when both banks were forested, it was significantly greater than BPRL. BTWRD ($P < 0.05$) and BRND ($P < 0.10$) also contributed more LWD to the channel than BPRL. OTWRD yielded more LWD than OPRL, ODEF, and ORND (35 percent, 50 percent, and 52 percent of OTWRD's cumulative LWD total, respectively), while OQRT provided more ($P < 0.10$) than OPRL. The ORND, ODEF, and OPRL treatments did not differ statistically.

Discussion

Although these bank afforestation and snag fall patterns are greatly simplified, their influence on LWD recruitment is statistically and ecologically meaningful. Random or tri-modal (i.e., CWD default) patterns produced intermediate levels of recruitment, while fall patterns biased strongly in particular directions resulted in either greater or lesser delivery, depending on bank afforestation and the predominant snag failure direction.

With only one forested bank, both the magnitude and the absolute volume of LWD recruited were substantially decreased *(table 1).* Three of the simulated patterns (ORND, ODEF, and OPRL) yielded about 50 percent less debris than their well-forested counterparts. Rather than uniformly decreasing by half the LWD recruitment totals, the biased patterns tending towards the channel (OTWRD and OQRT) experienced a decrease of only 15 to 20 percent, suggesting that snags falling along the major axis are the most important component of riparian LWD recruitment.

Conclusions

This research showed that bank afforestation and snag angle-of-fall significantly influenced riparian LWD recruitment. Unfortunately, very few simulation studies have accounted for the impact of streamside forest coverage and snag fall when predicting long-term woody debris dynamics. With both banks forested, a greater volume of LWD was delivered over the simulation period, while snag failure patterns biased towards the stream outproduced random or other patterns not favoring the channel. Snag angle-of-fall became critical when only one side was forested and a strong unidirectional control (e.g., prevailing winds) was present.

Acknowledgments

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Modeling the Delivery of Large Wood to Streams with Light Detection and Ranging (LIDAR) Data[1]

William Cody Fleece[2]

Abstract

A remote sensing technology called Light Detection and Ranging (LIDAR) was used to assess the characteristics of streamside forest structure and predict the delivery of wood to over 55 stream kilometers in a 28-square kilometer study area. The LIDAR data correlated with canopy height ($R^2 = 0.65$) and stand average basal area ($R^2 = 0.45$). The model predicted that 83 percent of wood delivered to streams originated within 20 meters of the channel and that 95 percent came from within 30 meters of the channel.

Introduction

Modeling the rate of large wood delivery to streams over large areas is not practical because the forest structure information required is frequently unavailable. Recent advances in remote sensing technology can now provide resource managers with the ability to characterize the structure of streamside vegetation and model the loading of wood to streams. The objective of this study was to use Light Detection and Ranging (LIDAR) data to model the delivery of wood to streams within the study area. This was accomplished by first transforming raw point elevation measurements to gridded surfaces. These surfaces were then compared to ground-based forest structure information in order to determine if the LIDAR data accurately characterized forest structure. The LIDAR data was used for two of three variables needed in a wood delivery model.

Large wood is an integral part of many stream ecosystems in the Pacific Northwest. A wide variety of organisms have life histories associated with wood located in the active channel. It is a substrate for photosynthetic organisms such as green algae, cyanobacteria, diatoms, liverworts, mosses, and trees (Harmon and others 1986). Large woody debris jams often create low velocity lateral habitats, which provide resources and refugia for juvenile fish (Moore and Gregory 1989). Streams with large pieces of wood in the active channel better retain dissolved and particulate carbon than those without large wood (Bilby 1981, Bilby and Likens 1980). In addition to the chemical and biological interactions mentioned above, large wood is a key factor in determining the geomorphic response of a stream to the

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physical disturbances that shape the channel. There is a positive relationship between pool volume and the amount of large wood in the channel (Carlson and others 1990). Energy dissipation of streamflow caused by the presence of wood dams causes the formation of upstream gravel bars (Lisle 1986).

Most large wood delivered to streams originates in the streamside vegetation. In fact approximately 80 percent of the wood in western Oregon Cascades streams was delivered from within 20 m of the active channel (McDade and others 1989, Van Sickle and Gregory 1990). Murphy and Koski (1989) reached similar conclusions for some Alaskan streams, but the distance of origin was less than that reported in the previously mentioned studies. Difference in tree height is the likely cause of this disparity.

Timber harvesting adjacent to streams has, in many cases depleted the source of large wood pieces. Consequently many of these streams now have fewer large pieces than streams with undisturbed riparian stands (Bilby and Ward 1991). In some cases the harvested stands supply a greater number of wood pieces. These pieces, however, are smaller and highly mobile compared to downed wood in the streams of old-growth forests (Evans and others 1993, McHenry and others 1998).

Estimating the delivery of wood to streams by means described in traditional methods requires detailed information on stand structure (i.e., the height of every tree and its distance from the stream) (Minor 1997, Van Sickle and Gregory 1990). Alternatively, loading may be estimated by surveying a stream over a period of years and recording wood inputs (McDade and others 1989). This information is not readily available for many forested streams. In cases where the required information is available, it is often limited to very small spatial extents. This study seeks to determine whether a remote sensing technology called Light Detection and Ranging (LIDAR) can provide information necessary to predict wood delivery to streams over a wider spatial extent than is practical with ground-based methods.

Study Area

This study was conducted in the McDonald-Dunn State Research Forest (McDonald-Dunn Forest) near Corvallis, Oregon *(fig. 1)*. The McDonald-Dunn Forest is located in the Valley Foothills subecoregion of the Willamette Valley ecoregion. The Valley Foothills range in elevation from 10 to 1,500 feet and receive 40 to 60 inches of rain per year (Pater and others 1997).

The McDonald Forest comprises approximately 48 square kilometers and within its boundaries are more than 30 different tree species, including *Abies grandis*, *Pseudotsuga menziesi,* and *Quercus garryana*. The majority of stands in the McDonald-Dunn Forest are either coniferous or a coniferous/hardwood mixture. Only 13 of 179 stands are greater than 200 years old, and the median stand age is roughly 60 years. The LIDAR flight line and the 28 square kilometer study area include portions of the McDonald-Dunn Forest as well as some privately owned land. Approximately 55-kilometers of stream occur within the study area, most of which are first-order and second-order streams. The largest stream, Soap Creek, is fourth-order and lies on the eastern boundary of the study area.

Figure 1—The study area in the McDonald-Dunn State Research Forest near Corvallis, Oregon.

LIDAR Technology

LIDAR is a remote sensing technology capable of characterizing a variety of vegetation structure metrics. Studies have shown LIDAR capable of accurately measuring mean canopy height (Magnussen and Boudevyn 1998, Naesset 1997), timber volume (Naesset 1997, Nilsson 1996), basal area (Lefsky and others 1997, Means and others 1999), and biomass (Lefsky and others 1999, Nelson 1997). LIDAR is also used for characterizing topography (Garvin 1996). LIDAR technology is based upon the general principle that a portion(s) of an emitted laser pulse will reflect to its source. Because the travel rate of a pulse is constant (i.e., the speed of light), concurrently emitted pulses with different return times must have differing travel distances. Portions of these pulses reflect back to a sensor on the airplane. Because the position and orientation of the sensor is known for each emitted pulse, every returning signal has a unique set of three-dimensional coordinates.

The LIDAR unit used for this study is a scanning system. Approximately 15,000 pulses per second were emitted in a sinusoidal pattern *(fig. 2)* from an airplane at an altitude of 2,000 m. The footprint, or size of the laser pulse upon reaching the earth, was approximately 0.5 m in diameter. The spacing between pulses over bare earth was approximately 6 m, and the width of each scan was approximately 4,500 m. Because the same pulse can generate several returning signals, the distance between points, in the horizontal plane is often less than 6 m. Multiple returns are generated when some portion of a laser pulse is intercepted by a reflective surface and returned to the airborne sensor. The uninterrupted portion of the pulse can generate additional return signals if reflective surfaces are encountered.

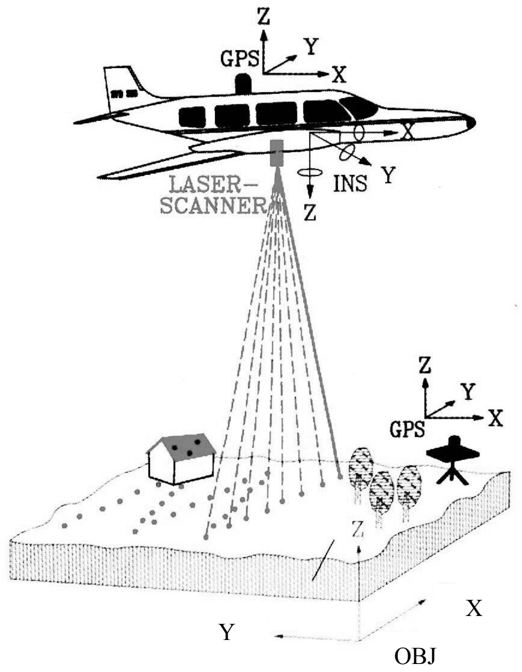

Figure 2—Airborne laser scanner.

Methods

The objective of this study is to use LIDAR data to model the delivery of wood to streams within the study area. To accomplish this, LIDAR was first transformed to gridded surfaces representing the ground and canopy surface. These surfaces were then compared to ground-based forest structure information in order to determine if LIDAR accurately characterized forest structure. LIDAR was then used to derive two of three variables in a probabilistic wood delivery model.

Airborne Data Collection

Airborne data were collected in October 1998. The number of returning signals was highly variable. A single returning signal was most common. Second and third returns were also very common but respectively less frequent. Fourth or fifth returns were captured in rare instances.

Number of return signals for study area:

Signal return order	No. of signals
1st	992,208
2nd	200,611
3rd	27,784
4th	2,068
5th	89

One explanation for the decreasing number of signals with return order is technological. There was a limit on the speed at which return signals were assimilated. The scanning equipment is capable of capturing only one signal every 0.2 nanoseconds. Once a signal was recorded, additional capture was precluded for a time that equated to approximately 5 m of travel distance. Therefore, only vegetation greater than 5 m in height can generate multiple returns from a single pulse.

Ground Data Collection

Two ground-based data sets were used in this study. The first was a set of ground plots, and the second was a stand-level aggregation of ground plot data. The ground plot data used in this study were collected as part of an ongoing forest inventory at the McDonald-Dunn Forest. Data collection occurred between July 1997 and February 1998. All sample plots have a variable radius. Tree size and distance from a reference center point determine the radius of these plots. All trees equal to or greater than 20-centimeters in diameter at breast height (DBH) and located within 6.1 m of the plot center were automatically included in the sample. Large trees located beyond the 6.1 meter threshold were included in the sample if the DBH was sufficiently large. Either prisms or relaskops were used to identify trees for inclusion in the sample (Oregon State University 1999). Among the recorded measurements were DBH and tree heights. Tree heights were recorded for all living and dead trees within the plot.

The stand data used in this study were derived from the ground plot data and digital orthophotographs. Ground plots with similar characteristics (e.g., height, age) were grouped together and stand boundaries were digitized around those clusters based on the features observed in the photographs. These groupings contain the attribute summaries of information collected at the plot level including, but not limited to, basal area. Since not every ground plot was sampled every year, where current stand information was missing, a growth and yield model called ORGANON was used to simulate the growth of individual trees from the last period of record to the present date. The return interval for sampling an individual ground plot is typically less than 10 years but can vary from 1 to 15 years.

Airborne Data Transformation

Each LIDAR return signal contains a unique three-dimensional coordinate. Ground elevation return signals were separated from return signals generated by the vegetation via a proprietary processing algorithm (Renslow, pers. comm.). Generally described, this process works as follows: 1) last return signals are separated from non-first return signals, 2) a Triangulated Irregular Network surface (TIN) is created from these points, 3) points obviously above the ground were removed on the basis of visual inspection, 4) the process is repeated until all points above the ground were removed. Digital orthophoto stereo pairs were used to verify the categorization of these signals. Triangulated Irregular Network surfaces (TINs) were computed from the x, y, and z coordinates of the ground and first return LIDAR point files. A TIN is a set of non-overlapping, adjacent triangles intersecting the points with three-dimensional coordinates *(fig. 3)*. The TINs in this study were used to generate gridded surfaces called lattices. Lattices are similar to TINs in that the mesh points contain elevation information. The spacing and resolution of these two data models, however, is very different. The mesh points of a TIN contain information from the original point files. Mesh points do not exist between the original raw point locations. In the conversion from TIN to lattice, mesh points are created at regular intervals. Interpolation is used to calculate the mesh point elevation where the distance between original points is greater than the resolution of the created lattice. The principle advantage of a lattice over a TIN is that calculations can be performed on lattices, whereas this capability is not available for TINs. After creation of the lattices, the ground elevation surface was subtracted from the first return elevation surface. The result of this calculation was a new lattice for which each cell contained a canopy height value. The cell size for each of these surfaces is approximately 1.5 m.

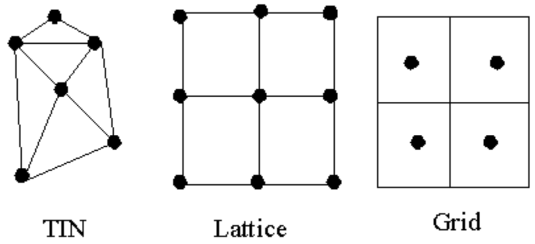

Figure 3—Data model structure.

Thirty-two ground plots in a 929-hectare section of the southwestern portion of the study area were selected and compared to the canopy height grid. This section of the study area was selected because it contained the full range of forest structure characteristics, from very old to very young. Ground plots located adjacent to roads or clear cuts were excluded from the analysis because of uncertainties regarding the geographic location of the plot's GIS data set. The heights of individual trees in each ground plot were averaged, and the values were plotted against the laser-derived canopy height *(fig. 4).*

The rate of large wood delivery, to streams, predicted by the model in this study was compared to wood delivery rates observed in the Western Cascades ecoregion (Lienkaemper and Swanson 1987). Five hundred-year-old conifer forests surrounded the streams in the Cascade study. The Cascade sites are higher in elevation and receive more precipitation than the McDonald-Dunn Forest. Differing environmental conditions may influence the result of any comparison. However, these forests (especially the older forests) have structural similarities that may make a comparison useful. Many of the tree species such as Douglas-fir *(Pseudotsuga menziesii)* are common to both study areas. Trees in the Cascade sites are likely to be larger than trees in the McDonald Forest, resulting in larger source areas.

Lienkaemper and Swanson (1986) recorded the number of trees entering five streams over a period of 7 to 9 years. From this information I calculated the number of trees entering the stream per hectare of source area over a 5-year period. I assume that all the trees entering the Cascade streams had origins less than 35 m from the channel (McDade and others 1989). This may be a conservative estimate considering that McDade (1988) observed evidence of trees falling into streams from distances greater than 60 m.

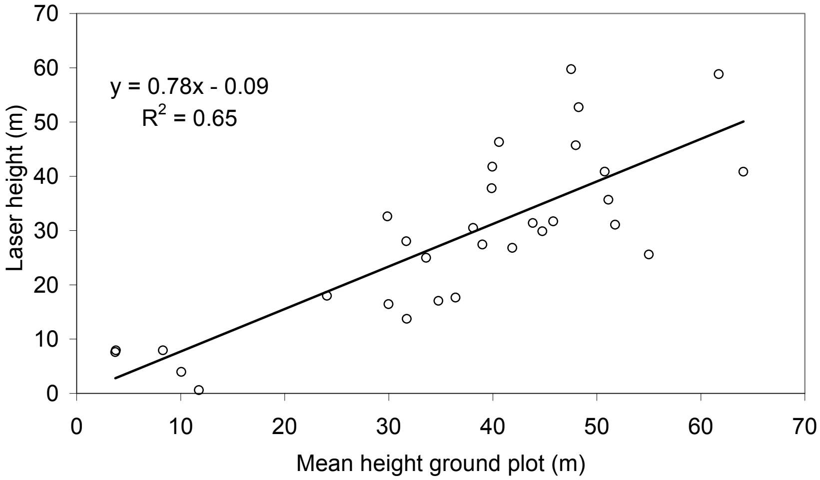

Figure 4—Ground plot height vs. laser height.

The Wood Model

Unlike most wood delivery models, data used in this study are not tree specific. LIDAR data do not provide information about individual trees. Instead, LIDAR defines a surface(s) that approximates tree height. The resolution of each of these surfaces is approximately 1.5 m. Therefore, the model in this study describes the probability that a given cell will deliver wood to a stream. Delivery of wood to streams is characterized by the equation:

$$W_d = P_s \, D \, R_f \tag{1}$$

The delivery of wood to a stream is represented by (W_d) and is expressed as the number of trees falling in a stream per hectare over a 5-year period. P_s equals the probability that a tree will fall in a stream given the height of the tree and its distance from the stream. D is a relative measure of tree density and is unit-less. R_f, the rate of tree fall, equals the average number of trees that fell per hectare over a 5-year period.

Probability of Falling in a Stream

The probability of a tree falling in a stream is a function of tree height and distance from the stream. It is assumed that the direction of tree fall is random. The probability of a given grid cell contributing wood to a stream (P_s) is based on the trigonometric function:

$$P_s = (\text{arccosine} \, (z / h)) / 180 \tag{2}$$

in which the variable z equals the perpendicular distance to the stream and h equals the height of a given cell. A geographic information system (GIS) was used to obtain both variables for this equation. Using GIS, a grid was created to compute the shortest perpendicular distance to a given segment of the stream network. It was not possible to calculate the distance to two streams. Therefore, it is necessary to assume that when a tree falls it always falls in the nearest stream. A visual assessment of the study area showed that only a small number of canopy height grid cells could potentially contribute to two streams (i.e., near confluences); thus, this was not expected to affect the model results.

Density

Density in the wood delivery models (Minor 1997, Van Sickle and Gregory 1990) is the number of trees per unit area. In this study an alternative approach was taken because of the inability to discern individual trees with this LIDAR data set. I hypothesized that a relationship between the density of LIDAR return signals, per unit area, and forest density might exist.

Because first return signals are so numerous (one flight line of approximately 6-miles in length contained more than 5-million first return points) and because even clearcuts generate first returns, these points were eliminated from the density analysis. A grid was created to represent the density of non-first return points per unit area. The point density computation counted every LIDAR point within a 0.4-hecare area (equivalent to a circle 36m in diameter). The results of this analysis were converted to points per hectare that were then compared to stand averages for basal area *(fig. 5)*. Basal area was used here as a relative measure of density. I then used the relationship observed in *figure 5* and equation 3 to assign the stand average basal area to every grid cell in the study area.

$$\text{Basal Area} = (\ln(\text{dnst-grd} / 36.594)) / 0.0248 \tag{3}$$

This equation yielded the basal area in square meters per hectare. The fraction of basal area (BA) per cell was calculated as:

$$D = (BA \text{ m}^2 / \text{ha}) * (1 \text{ ha} / 10{,}000 \text{ m}^2) \tag{4}$$

This value was used as density in the total loading calculation.

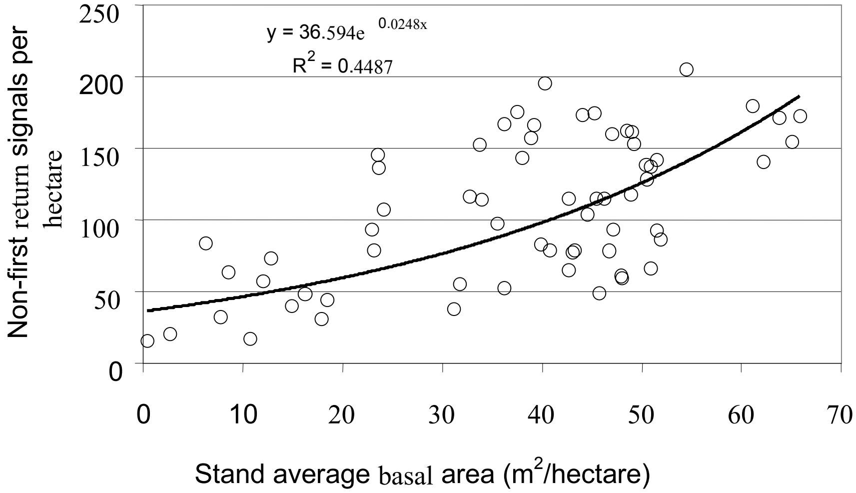

Figure 5—Basal area vs. non-first return signals.

Rate of Fall

No direct estimate of tree fall was available for this study. Van Sickle and Gregory (1990) used mortality as a rough approximation of the probability of tree fall. ORGANON, a model designed to predict the growth of individual trees in a stand, is also capable of estimating mortality for all trees less than 109-centimeters in diameter. I assume for this study that the probability of tree fall equals mortality, thus no trees were snags after mortality. ORGANON and input files for every stand in the McDonald Forest are available at the Web site: http://www.cof.orst.edu/resfor/mcdonald/purpose.sht.

The data from 30 stands within the study area were randomly selected as input files for ORGANON. The model is designed to run with greater than 50 trees per stand. Twenty of the initial 30 stands did not meet this requirement and were discarded. Growth over a 25-year period was calculated for each of the remaining input files:

Stand No.	**Mortality** [1]
61103	56.049
60802	56.148
60513	81.259
60811	111.901
70501	133.457
60402	198.346
60403	209.580
51101	259.951
51001	325.062
60901	334.272
Average/25 yrs.	176.603
Average/5yrs.	35.321

[1] Number of trees/hectare for 25-year period.

The average mortality of all 10 stands was calculated for a 5-year period and applied uniformly across the study area as an approximation for the rate of fall (R_f). A uniform R_f was used in the wood delivery model, though it is recognized that mortality is highly variable and site specific. The 5-year time period was chosen because the results of this model will be compared to data collected in the western Cascade Mountains over a similar time interval.

Results

The cumulative frequency of wood delivered to streams, as a function of distance from the stream, is a value commonly reported in wood delivery studies (McDade 1988, McDade and others 1989, Minor 1997, Van Sickle and Gregory 1990). This study found that 83 percent of the predicted wood delivered to streams came from within 20 m of the channel, and 95 percent came from within 30 m of the channel *(fig. 6)*. Murphy and Koski (1989) found that 99 percent of the wood in southeast Alaska came from within 30 m of the channel. McDade (1988) reported that roughly 90 percent of wood delivery to streams in 29 old growth forests in Oregon and Washington originated within 30 m of the stream. It is not surprising that the cumulative frequency distribution curves presented in this study report greater cumulative percentages from shorter distances than those reported in McDade (1988) because the stands in the McDonald-Dunn Forest, on average, are much shorter. Only thirteen of 179 stands studied were greater than 200 years old. The median age of the stands within the study area was approximately 60 years.

The model in this study also predicted the rate at which large wood enters streams. These predictions were compared to values reported by Lienkaemper and Swanson (1987). Predictions from the McDonald-Dunn Forest closely match those of the H.J. Andrews Research Forest *(table 1)*. The values for Lookout Creek may be lower than expected due to the presence of a road in the source area. The value reported for the McDonald-Dunn Forest is the mean of the entire study area. Further investigation of loading rates from specific stream segments and from various stand structure types is needed.

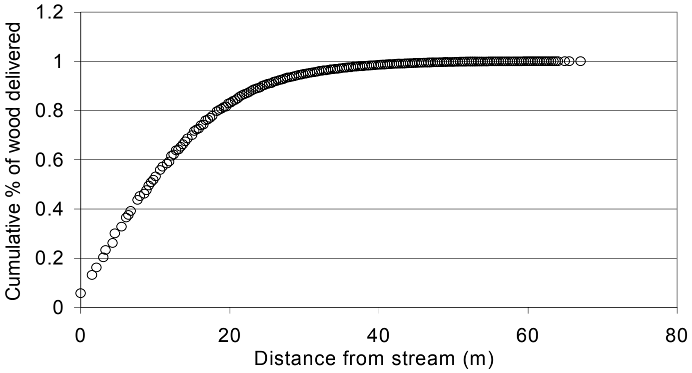

Figure 6—Wood recruitment as a function of distance from the stream for the entire study area.

Tables 1—*Loading Rate Comparison between H.J. Andrews Research Forest and McDonald-Dunn Forest.*

Location	No. of years	Reach length	Width[1]	Area (ha)	No. of trees added	Trees/ha	Trees/ha 5-yr. period
ws-9[2]	8	170	70	1.19	6	5.0420	3.1513
ws-2[2]	8	146	70	1.022	4	3.9139	2.4462
Mack Creek[2]	9	332	70	2.324	10	4.3029	2.3905
Upper Lookout[2]	9	483	70	3.381	12	3.5492	1.9718
Lower Lookout[2]	7	350	70	2.45	6	2.4490	1.7493
McDonald-Dunn Forest[3]							3.0035

[1] Assumed source-area based from McDade and others 1989.
[2] Numbers derived from values reported in Lienkaemper and Swanson 1986.
[2] Average for entire study area.

Discussion

The ORGANON mortality values used in this study were not spatially explicit. ORGANON calculated mortality values for a wide range of age classes. With the aid of height regression equations, mortality could be applied variably across the landscape based on the canopy height observed in each grid cell. This approach might be warranted because Headman and others (1996) found that loading rates varied with stand age, indicating that mortality is lowest for moderately aged stands. Further, this study utilized only a small portion of the total number of stands. As illustrated, mortality varies from stand to stand. Mortality values could potentially be associated with the geographic location of each stand. Because this approach would not be practical in remote areas with little stand data, it was not pursued in this study.

The delivery rate value reported in this study was a mean for all 55 stream kilometers. The delivery rates reported in the Lienkaemper and Swanson (1987) study were for comparatively short stream reaches of a few 100 meters. Most of the stands in the McDonald-Dunn Forest are much younger and shorter than those studied at the H.J. Andrews Forest. Although these results are encouraging, further evaluation of model predictions for shorter stream reaches in the McDonald-Dunn Forest is warranted.

Conclusion

A strong correlation was observed between the ground plot forest structure metrics and laser derived canopy height. A relationship was also observed between the stand average basal area and the number on non-first return LIDAR points. The cumulative frequency distribution curve and the wood delivery rate predicted by this model are consistent with the conceptual frameworks established in other studies. Additional research is needed to refine the ability of this technology to assess the wood delivery potential of streamside forests, but initial results are promising.

Although the scope of the modeling in this study was limited to wood delivery, LIDAR technology shows great potential as a tool in the study of stream ecosystems. Some potential applications are stream shading studies, litterfall modeling, quantification of the area of streamside forests that can potentially deliver wood to streams, and a number of topographic applications. Because LIDAR data can be collected over such large areas, it shows great promise as a watershed assessment tool.

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How Much Dead Wood in Stream Channels Is Enough?[1]

Thomas E. Lisle[2]

Abstract

Private forest managers often seek guidelines on how much dead wood should be retained in streams in order to adequately fulfill ecosystem functions. There are three approaches to answering this question for a particular reach of channel. The first approach uses an understanding of *ecologic functions* of dead wood in streams to determine the amount needed to fulfill ecologic and geomorphic functions. This approach fails because the complexities of sizes, shapes, and arrangements of dead wood in a variety of lotic ecosystems overwhelm any scientific specification of target loadings. Another approach uses *reference loadings* to evaluate departures in amounts of dead wood in streams from reference amounts in unaltered systems. A precise threshold cannot be defined using this approach because dead wood volumes are highly variable, even within pristine channels in similar settings, and distributions for managed and pristine channels overlap. A third approach constructs a *wood budget* by evaluating past, present, and projected supplies in streams and riparian areas. This is a cumulative-effects analysis that shifts the focus from channels to riparian forests. In combination, the three approaches provide the best information to determine how much wood is enough, but they do not offer simple, formulaic prescriptions. The demands for performing the necessary analyses before harvesting riparian wood suggest that management of riparian forests will continue to be guided most often by general prescriptions.

Introduction

A primary goal of managing riparian forests is to maintain sufficient dead wood in stream channels so that it fully performs its natural geomorphic and ecologic functions. Much is at stake in balancing the economic and ecologic values of riparian wood. Today, most land managers appreciate the value of dead wood in large fish-bearing channels, although less is known or appreciated about its value in low-order, intermittent tributaries. This gap is critical because first- and second-order channels comprise a large portion of the drainage network; in sixth-order drainage networks, for example, such low-order channels account for roughly two-thirds of the total channel length. The economic value of riparian wood can be evaluated from the market, although the profit realized by a timberland owner is uncertain, due in part to evolving regulations. The ecological value cannot be evaluated as precisely because of the complexity and variability of riparian conditions and processes supporting the functions of dead wood in aquatic ecosystems. How do we weigh the economic and ecologic contribution of riparian wood and manage riparian forests under some inevitable uncertainties?

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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In the 1994 Northwest Forest Plan (FEMAT 1993), Federal agencies managing forests in the Pacific Northwest pled ignorance of natural processes and gave guidelines for setting aside riparian reserves in which direct pathways of watershed products (water, sediment, wood, heat, and nutrients) to aquatic ecosystems would not be disturbed by human activities until those pathways were analyzed and understood (e.g., watershed analysis; FEMAT 1993). Although the implementation of these guidelines remains controversial, this strategy greatly simplifies management decisions in riparian reserves once they are designated. In contrast, many private forest owners press to limit the size of buffer strips and continue entering riparian forests to harvest timber. Extracting riparian wood without significantly impacting lotic ecosystems requires more active management strategies and motivates better understanding of the dynamics and functions of dead wood and other functions of riparian forests for aquatic ecosystems. The private forester might phrase the problem as: “How much wood should I retain in order to satisfy the ecologic functions that society demands?”

This question can be analyzed by using three approaches:

1. *Ecologic functions*: Determine the amount of dead wood in streams needed to fulfill vital functions, e.g., maintaining habitat for a sensitive species.
2. *Reference loadings*: Determine desired amounts of dead wood in streams from amounts in unaltered systems.
3. *Wood budgets*: Determine desired amounts in streams and riparian sources by constructing a wood budget to evaluate past, present, and projected supplies.

In this paper, I evaluate these approaches and present a new compilation of data on dead wood volumes in California and Oregon.

Approach 1: Ecological Functions of Dead Wood

The great variety of functions of dead wood in lotic ecosystems is summarized elsewhere (Harmon and others 1986, Sedell and others 1988), and I will mention only a few here for the sake of discussion. In general, lotic communities have evolved with natural and variable supplies of watershed products, including large quantities of wood in forested streams. Dead wood is commonly the most important source of structure in forest streams. It also affects the routing of other watershed products, particularly sediment, and their influence on ecosystems. By concentrating and dispersing hydraulic forces, dead wood can greatly diversify physical conditions in streams and provide habitats for various species and age classes in aquatic communities.

A salient characteristic of dead wood in channels is its variability in terms of supply, longevity, and function. The diameter of dead wood is commonly larger than bed particles by an order of magnitude or more and comparable in scale to channel depth; wood length is comparable to channel width. Thus, single pieces can locally control channel morphology. Consequently, the myriad of sizes and shapes of dead wood can create a myriad of channel forms at the reach scale, depending on the arrangement of the wood and the background geomorphic and hydrologic conditions of the channel. One must be careful not to discount the variety of functions of dead wood in aquatic and riparian ecosystems. Nevertheless, the population of dead wood as distributed naturally in channels is highly inefficient in performing some easily recognizable functions for habitat. On the one hand, a single piece can strategically lodge along a channel thalweg at the outside bank of an incipient bend and thereby scour a deep pool. But more wood is likely to hang up on a bar or flood plain and interact with the flow only during flood stages. Thus, the influence of a single piece can vary widely as it moves downstream.

Moreover, dead wood in channels tends to be concentrated. Common wood input processes—wind storms, wildfire, landslides, and debris flows—quickly deliver large amounts of wood at points in the channel network. Even if inputs are widespread, fluvially transported wood tends to aggregate (Braudrick and others 1997). Although deposited aggregates (debris jams) can strongly affect channels, the obvious influence of individual pieces diminishes quickly with growth of the aggregate.

I do not mean to imply that there is plenty of wood to spare in streams, but that it is impossible to practically and scientifically specify how much is enough. The diversity of size and arrangement of wood and the diversity of channels makes it futile to say how a given amount of dead wood will result in particular habitat conditions. Effects are complex and stochastic. On the one hand, channels without dead wood or other forms of structure can quickly evolve to very simple forms. Moderately sized channels with gradients of about 1 to 4 percent are particularly prone to simplify, because they have a weak tendency to form bars and pools without exogenous structure (Montgomery and Buffington 1997). These conditions typify fish-bearing streams in managed forests in the west. On the other hand, the typically large volumes of dead wood in pristine forest channels contribute to diverse habitats. There is no scientifically defensible, site-specific way to determine what smaller amounts would adequately perform the same functions. For channels in intensively managed private forests, where is the middle ground? This type of uncertainty was the motive in the Northwest Forest Plan for setting aside riparian reserves with strong limitations on entry.

By using approach 1 alone, we are presently incapable of resolving the issue of how much wood is enough. Approach 1 motivates further research and conscientious, site-specific management of streams. By exploring the functions of dead wood in aquatic ecosystems, it provides a scientific basis for managing forest streams. However, it offers no simple prescriptions for the broader, regulatory arena.

Approach 2: Reference Values of Dead Wood Loading

Another approach to determining how much dead wood is enough is to compare volumes and sizes in a given channel to those in comparable channels that serve as references. Given that aquatic communities evolved long before intensive forest- and waterway management began, pristine channels offer the obvious reference condition. Management within the range of pristine conditions provides a level of confidence that natural communities will persist. Although this reference may not always be attainable under management, it provides a standard to measure departures from natural conditions. To apply this approach, we need to know how the volume and size of dead wood varies between regions and within a region, and how management affects those variations.

Let us consider dead wood volumes first. I compiled frequency distributions of in-channel volumes of dead wood (m^3 per ha of bankfull channel area) in unmanaged forests in different climatic regions of California and Oregon *(fig. 1)*. Distributions in each region were compiled from a small sample of 9 to 12 reaches that were at least 200 m in length. The channels are second- to fourth-order; drainage areas range from 50 to 3,000 ha. Because these reaches were not selected randomly, they do not represent an unbiased sample of pristine conditions. Despite these limitations, the data show some expected trends. There are wide differences between regions. For example, the median loading for old-growth redwood is about 1,000 m^3/ha, while median loading for mixed conifers in the northern Sierra Nevada is only 30 m^3/ha. This indicates that reference (or pristine) loadings for one region must not be applied to another. There are also wide variations within regions; the difference between minimum and maximum loadings is well over tenfold in each region.

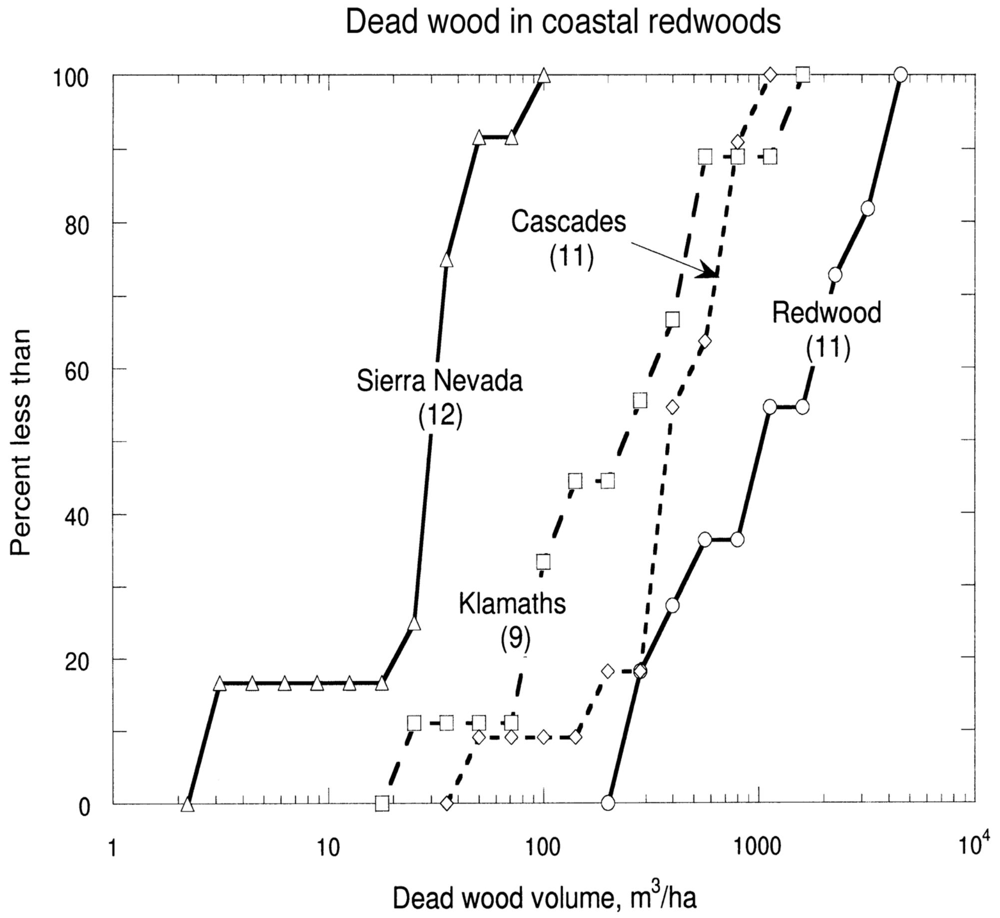

Figure 1—Cumulative frequency distributions of volumes of dead wood in pristine channels in four forest types: Oregon Cascades and Klamath Mountains (Harmon and others 1986); coastal redwood (Keller and Tally 1979); and Sierra Nevada (Berg and others 1998). Number of channels in the sample are given in parentheses. Study reaches are at least 200 m long.

Within coastal redwood forests, management has clearly reduced dead wood volumes in streams. Channels flowing through managed redwood forests contain two to five times less wood than old-growth channels for a given cumulative percentage *(fig. 2)*. A history of logging, log running, salvage, and stream cleaning has apparently created a deficit of wood in channels. However, as is common with environmental parameters, distributions for managed and unmanaged channels overlap. Although there is a clear departure of managed channels from pristine conditions, a comparison of frequency distributions is not very useful for prescribing target loadings for individual channels. For example, using a "natural-range-of-variability" criterion could suggest that loadings of 200 m^3/ha in managed channels would meet "natural" conditions since such low loadings are represented in at least one old-growth channel. However, such a prescription would tend to increase the wood deficit on a regional scale, because improvement would be prescribed only for the 20 percent of managed channels having the lowest loading. On the other hand, a prescription of the median old-growth loading (1,000 m^3/ha) might substantially decrease the regional deficit, but would be unachievable in most managed channels since one-half of the old-growth channels (nearly all in reserves) would already be "in violation." A single-valued prescription for woody debris loading, even in the same forest type, is therefore unworkable.

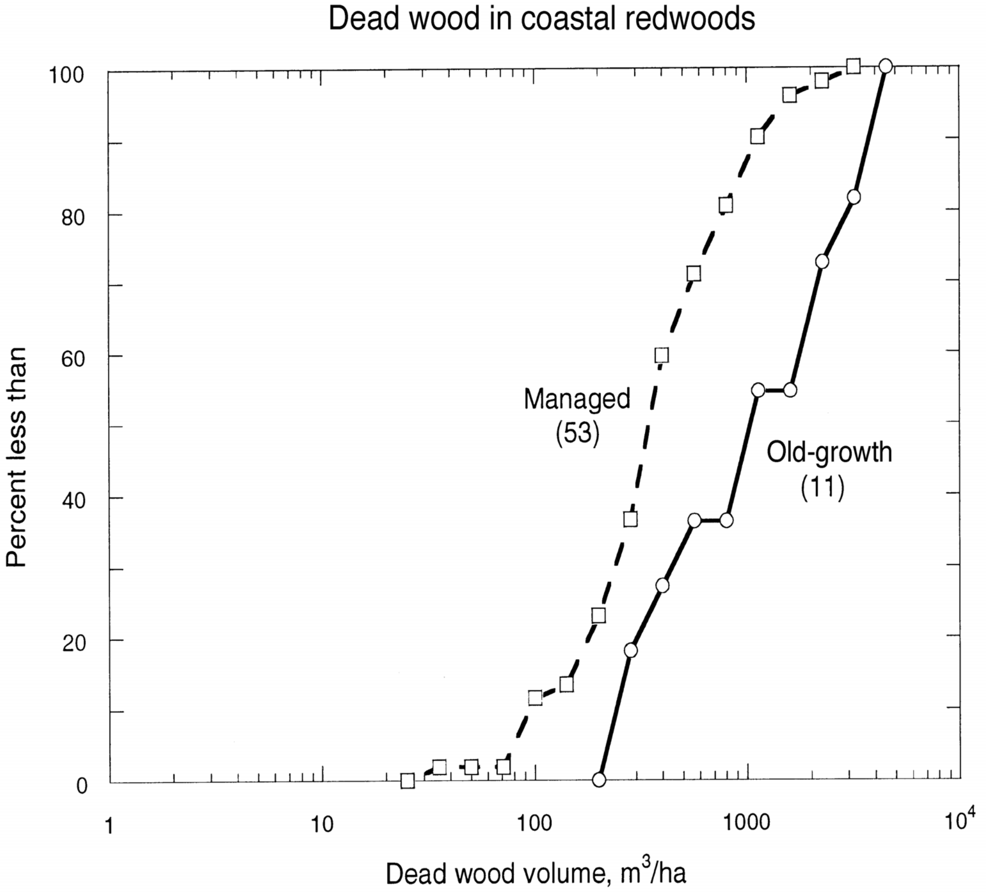

Figure 2—Cumulative frequency distributions of volumes of dead wood in channels in managed (Knopp 1993) and old-growth (Keller and Tally 1979) coastal redwoods. Number of channels in the sample are given in parentheses. Study reaches are at least 200 m long.

Differences in wood size between pristine and managed streams are probably also pronounced. As large, old-growth dead wood in managed streams decreases through decay, salvage, cleaning, and mobilization, it is replaced by smaller wood from managed stands. The size difference is important because big wood lasts longer and affects channels more strongly. The difference is exemplified in a comparison of frequency distributions of the volume of individual pieces of dead wood in two third-order, coastal redwood channels having similar drainage areas: Little Lost Man Creek (Keller and Tally 1979), an old-growth channel, and North Fork Caspar Creek, a second-growth channel *(fig. 3)*. Old-growth wood in Caspar Creek was nearly eliminated by splash-dam operations at the turn of the century, and second-growth forests have since supplied wood without human intervention (Napolitano 1998). For this analysis, the lower bound of piece size was set at 0.4 m^3. The frequency of small sizes (0.4-0.8 m^3) is similar, but frequencies diverge rapidly for larger sizes. The second-growth channel clearly has smaller wood.

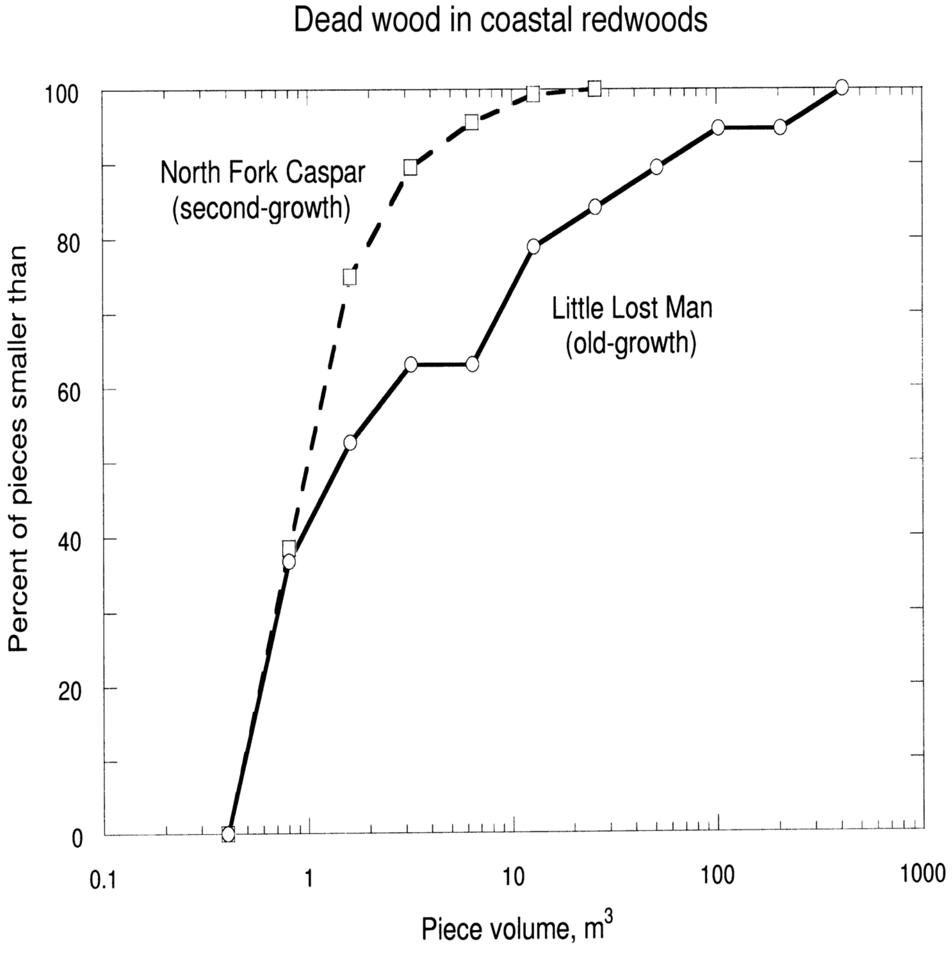

Figure 3—Cumulative frequency distributions of volumes of individual pieces of dead wood in two coastal redwood streams: North Fork Caspar Creek (second-growth) and Little Lost Man Creek (old-growth; Keller and Tally 1979).

Although approach 2 fails to prescribe uniform target loadings (and sizes), some general goals and directions for regional management for dead wood in aquatic ecosystems are clearly suggested. First, there is an apparent regional deficit in dead wood loadings that is probably affecting species such as coho salmon that benefit from wood-formed habitats. This could motivate regional goals to improve protection of in-channel and riparian supplies of wood. Second, the wide variation and overlap between wood loadings in managed and pristine streams suggest that site-specific analyses are needed to achieve these goals if riparian wood is to be harvested.

Approach 3: Dead Wood Budgets

One of the shortcomings of approaches 1 and 2 is that even if we knew how much wood in streams is enough, we would also have to know how to manage riparian forests to achieve that loading. Approach 3 widens the focus to wood supplies in riparian forests. Wood in streams is evaluated in context of the potential of the riparian forest to furnish adequate wood to the channel, given historical inputs and outputs that have culminated in the present loading. Then, current and projected trends can be evaluated under alternative management. By accounting for local variations in wood loading, approach 3 is the site-specific alternative to approach 2. Implicit in the analysis is the consideration of size as well as volume of wood. Approach 3 is essentially a cumulative effects analysis accomplished by constructing a wood budget (Surfleet and Ziemer 1996, Swanson and others 1982) to answer three questions:

- What accounts for present wood loading, and more specifically, how much has land use affected riparian sources and input and output mechanisms since intensive land use began?
- What is the trend in wood loading given the present and future potential of the existing riparian forest to contribute wood to the stream?
- How will management alternatives affect future loadings?

Although historic values for volumes of wood lost or gained usually cannot be determined precisely, enough can be learned of past events and conditions to roughly evaluate departures from natural loadings. This may be adequate to inform managers which alternative land use plans would be appropriate, given present and projected trends in wood supplies. For example, if there has been a history of wood depletion from log runs in the nineteenth century in a particular stream, followed by aggressive stream cleaning in the 1980s, then there would be added incentive to maintain recovering supplies in managed riparian stands. Wind throw from narrow buffer strips might provide short-term increases in wood, but early cashing-in of remaining wood supplies could perpetuate the deficit in future decades.

Wood size as well as volume must be considered in a wood budget. Sustainable supplies of old-growth wood are gone from most managed streams. In its absence, the effectiveness of smaller size classes of available wood to replace the functions of old-growth wood needs to be evaluated (approach 1). Perhaps some minimum effective size can be used to categorize size classes in a wood budget. Longevity is another important consideration.

A wood budget (approach 3), along with knowledge of the role of wood in that particular channel (approach 1) and its loading compared to that in other channels in the same forest type (approach 2), provide the best information to weigh land use alternatives. It correctly sets the stage for regulatory debate by shifting the focus on how much wood is enough from channels to the riparian zone. However, it does not provide a standard formula for making such a determination, but instead informs the debate.

Conclusions

Dead wood in streams in the Pacific Northwest is being managed in the context of conflicting interests of protecting sensitive salmonid populations and tapping riparian wood supplies for timber. This motivates the question: "How much dead wood in forest streams is enough?" Federal agencies in the Northwest Forest Plan effectively skirted this question in favor of salmonids by designating riparian reserves that, among other provisions, were intended to fully protect riparian supplies of dead wood for streams. The Federal provisions, applied over a wide area to important protected species, set an undeniable precedent. If not met on State and private land, an alternative strategy is needed: If habitat is to be adequately protected as riparian wood is harvested, then detailed, site-by-site analyses of dead wood and other habitat variables must be performed. I suggest that three kinds of information are needed for such analyses: the role of dead wood in forest streams and watersheds; relative volumes and sizes of dead wood in managed and reference streams in the same forest type; historical and projected conditions, events, and processes that control wood supply and longevity in riparian forests and streams. Together, they provide the best information to guide land-management decisions. However, analyses must be site-specific. Simple, effective, standardized prescriptions, formulas, or procedures requiring little understanding are not obviously forthcoming.

One cost of intensive management of riparian forests is to support site-specific analyses that could justify harvesting riparian wood. Adequate wood-based, cumulative effects analyses are unlikely to be done because first, such analyses would be costly and their conclusions contestable under the inevitable uncertainties outlined in this paper; and second, considering the widespread depletion of dead wood from streams in managed forests, these analyses are not likely to support harvesting much wood from riparian forests. Given this, general prescriptions of riparian preserves are likely to remain the primary approach to managing dead wood in streams. In the meantime, continued research into the three approaches should better inform general prescriptions and improve site-specific analyses. In particular, approach 1 provides the scientific basis for determining how much wood is enough; approach 3 leads to how this can be achieved.

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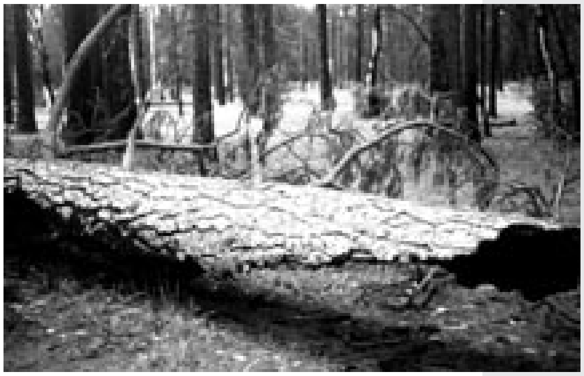
Importance to Invertebrates



An Investigation of the Insect Fauna Associated with Coarse Woody Debris of *Pinus ponderosa* and *Abies concolor* in Northeastern California[1]

Ethan Koenigs,[2] Patrick J. Shea,[2] Robert Borys,[3] and Michael I. Haverty[4]

Abstract

This study was initiated to determine the diversity and community structure of macroarthropods found in the coarse woody debris (CWD) of a pine/fir dominated forest. The USDA Forest Service has placed increased emphasis on understanding ecosystem processes that support long-term sustainability and biological diversity. Our study site was located in northeast California just west of the town of Tenant in the Klamath National Forest, Goosenest Adaptive Management Area (GAMA). We surveyed the arthropod fauna entering and emerging from CWD with three trap types: an acrylic pane trap with a water filled collection basin; a collar trap that wraps around a portion of a fallen log; and a solid plastic cylinder placed over stumps. Only data from the collar traps with the specimens identified to high taxonomic levels are reported in this paper. Equal numbers of traps were placed on white fir *(Abies concolor)* and ponderosa pine *(Pinus ponderosa).* Three stages of log decomposition, recently dead to soft but structurally intact, were sampled from each tree species. The insects from all traps were sorted to order, except for the Coleoptera, which were sorted to family or species level. The most numerous insects belong to the Order Diptera, followed by Coleoptera and Hymenoptera. Staphylinidae were the most numerous coleopterans, excluding the earliest decay stage in both tree species, where the Scolytidae were dominant. Termites, commonly found in CWD, were absent from all traps in all years.

Introduction

Much of the information on coarse woody debris (CWD) to date has focused on its importance as nutrient storage and as wildlife habitat (Bull and others 1997, Maser and others 1988). While mentioning the invertebrates associated with CWD and their potential importance in the decay process, few studies have attempted to elucidate the role they play. This study was designed to collect background information about

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insect diversity in this habitat type with the hope of providing methodologies and basic taxonomic data in the form of presence/absence and relative abundance for future research. Zhong and Showalter (1989) suggested that the rate of log decomposition could be influenced by the sequence of insect colonization and the micro flora brought in by these insects. Understanding the sequence of colonization is one of the first steps in understanding the role insects play in the decomposition process. Our long-term goals are to determine the diversity of insects associated with CWD; to assess the roles of various groups of insects found in CWD; and to provide analysis of various management strategies with regard to CWD inhabiting insects.

Additionally, most of the work on CWD to date has focused on the damp, coastal and western cascade forests of Oregon and Washington. Spies and others (1998), noted that to get a broader picture of the many roles of CWD, the range of sites needs to be expanded. This study in northern California should provide relevant information for many California forests.

There has been great attention in recent decades in preserving and maintaining our increasingly rare old-growth forests. Documents such as the *Sierra Nevada Ecosystem Project, Final Report to Congress*, exemplify this concern (Science Team 1996). We have recognized that these ecologically rich areas are critical to wildlife and that there is much to learn from them about maintaining sustainable forestry. To that end, some old-growth stands have been set aside in the form of National Parks and wilderness areas. Because of the mandate for sustainable forestry, management strategies will likely see a shift toward restoration. We do not want to de-emphasize the importance of preserves, for which there will always be a need, but restoration also holds great promise of regaining the diversity of wild lands. It offers us a chance to put into practice the lessons learned from natural areas by applying them to timber producing stands.

This project is part of a large, multidisciplinary ecosystem study on the Goosenest Adaptive Management Area (GAMA), northeast of Mount Shasta. The goal of the GAMA is to test methods of accelerating and restoring ponderosa pine old-growth characteristics through selective management. This study is being carried out on 20, 100-acre plots, which are being silviculturally managed to produce four treatments. These treatments include pine dominance with fire as a management tool; pine dominance with mechanical thinning; retain only large diameter trees regardless of species by mechanical thinning; control, or no silvicultural treatment. After these treatments have been initiated, the plots will be monitored for years to come, assessing the affects of each treatment on multiple parameters (wildlife, forest structure, fire effects, forest health, etc.). At present, our CWD insect emergence trapping has been conducted in areas near the study plots because of site availability and eastside pine/fir type mix suitability.

One aspect of old-growth is structural diversity. This refers to the forest canopy and the forest floor as well. A structurally diverse forest will have a variety of woody material at the soil surface providing habitat, nutrient recycling, and moisture to the forest. Once the plots have been created, we will be involved in monitoring the insects utilizing the CWD.

Study Site

The study site is located in northeastern California on the Goosenest Ranger district of the Klamath National Forest. The site is located on land designated as the GAMA. The landscape is characterized as rolling volcanic topography, typical of the Cascade province with elevations between 1,270 and 2,600 meters. The relatively dry climate reflects the topographic influence of the coastal mountains and the main thrust of the Cascades to the west. Most of the area receives 25-100 cm of precipitation that falls in the form of snow, with some summer thunderstorm rain contributing to the total (USDA 1996). As a result, the eastside ponderosa pine community dominates much of the GAMA. The area of study occurs in the transition zone between the eastside pine type and the coastal Douglas-fir *(Pseudotsuga menziesii)* type. This zone is dominated by a mixture of ponderosa pine *(Pinus ponderosa)* and white fir *(Abies concolor).*

Materials and Methods

Three types of traps were used in this investigation, but only data from the collar traps are presented here. To capture insects emerging from prostrate logs, traps were fashioned from a double layer of 95 percent shade cloth. The shade cloth was custom fit to cover 1-meter sections of logs of varying diameters. To ensure a relatively tight fit over the irregularities of the log and provide room for insects to travel under the shade cloth, the cloth was fitted over 10-cm-thick strips of medium density foam at both ends. Velcro strips were used to attach the shade cloth to the foam, to make for easy removal of the trap from the log. The foam strips were set 1 meter apart on the log and attached to the log with aluminum nails. Then the shade cloth could be laid across the foam, providing a space between the log and the cloth. The only source of light that insects could phototropically respond to was a glass mason jar fitted to the shade cloth on one side of the log. Emerging insects were attracted to the light and entered the jar containing a small insecticide impregnated chip containing 2,2-Dichlorovinyl dimethyl phosphate (DDVP). The insecticide kills the emerging insects before they can do damage to each other and make identification difficult or impossible.

To sample the insect fauna emerging from stumps, a modified 118- or 190-liter plastic garbage can was placed over the stumps, dependent on stump diameter. A medium hole was cut in the upper side of each can so that a transparent plastic funnel could be attached, large end toward the can. The funnel served as the only source of light inside the can, provided the only exit from the plastic can, and “funneled” the insects into a clear plastic collection cup. To prevent insects from leaving the cup or doing damage to each other, a similar insecticide impregnated chip, DDVP, was placed in the cup. In an attempt to lower the temperature inside the can, two square holes were cut in the side of the can and covered with shade cloth. This would allow some air movement inside the can to moderate temperatures without letting in much light.

To capture and sample insects from the surrounding environment, a clear acrylic sheet (pane trap), 0.5 cm thick by 80 cm long and 60 cm high, was placed against a down log bolted to upright aluminum brackets inserted into the ground. An acrylic collection tray, the same length as the pane trap, 14 cm wide and 10 cm high, was attached to the base of the pane and filled with soapy water to collect insects as they fell. A wire screen was placed over the collection tray to prevent birds and small mammals from removing insects from the traps.

Experimental Design

There were several specific objectives of this study. First, we wanted to develop effective sampling methods to detect insects utilizing stumps and fallen logs of various diameters. Then we hoped to compare the insect fauna found in white fir to that found in ponderosa pine. Finally, we wanted to compare the insect fauna across 3 decay stages, representing a continuum from recently dead to fairly decayed but maintaining shape. In the first year, 1997, our priority was to establish the effectiveness of the trapping technique. Because of this, the number and placement of traps was different than during the two succeeding years. In 1997, 54 emergence traps were deployed on a total of 18 logs, 3 traps per log. Of the 18 logs, 9 were ponderosa pine and 9 were white fir. Within each tree species, three trees in each of three decay classes (see below) were sampled. In 1998 and 1999, our trapping procedure changed after examining the 1997 data. To better compensate for variation, more trees (replicates) were sampled in each decay class. A total of 108 traps were deployed on 54 logs. With this arrangement, there were nine replications of each decay class for each species of tree. Thus, each trap covered a 1-meter section of log and with two traps per log, resulted in 18 meters of log being sampled from each decay class. This is twice the amount sampled in 1997 (3 logs x 3 traps/log x 1 meter/trap = 9 meters).

A total of 18 stump emergence traps were used in 1997, following the same pattern of three replications for each decay class in each species of tree. Because of the paucity of insects collected from these traps in 1997, the total number of traps was tripled to 54 in 1998, resulting in nine replications of each decay class for each tree species.

A total of 54 pane traps were used in 1997. Thirty-six traps were placed two per log on logs that contained collar traps. Another 18 pane traps were placed independently within the study area against down logs not containing color traps as controls. In 1998 and 1999, the amount of pane traps used was reduced to 18. One trap per log repeated three times for each decay class within both species. The large numbers of insects collected from the pane traps in 1997 precluded the use of as many traps in the following 2 years.

Decay Classes

The decay stage of each log was determined by using a set of modified parameters described by Maser and others (1979). Many investigators have used this classification system, likely due to the simple approach it uses to grade logs. In this system there are five decay classes based primarily on visual characteristics of the log**.** Class one has intact bark with intact texture. The log is round, twigs are present and the log is elevated on support points from broken branch stubs. Class two has intact bark with intact to partially soft texture. The log is round, twigs are absent and the log is elevated on support points or sagging slightly. Class three has partial or trace bark intact due to sloughing, with a texture of hard, large woody pieces. The log is round, twigs are absent and the log is sagging or portions on ground. Class four has bark absent with a texture of small, soft blocky wood pieces. The log is round to oval with portions of log on ground. Class five has bark absent with soft, powdery texture. The log is oval and on ground. We limited our survey of insects to the first three decay classes, in which most insect activity occurs (Harmon and others 1987). In classes four and five the log is becoming so soft that its quality as habitat for gallery forming insects decreases and the nutritive quality of the wood itself is also greatly diminished. At this point, decomposition is likely completed by fungi and microbes.

Stump Traps

The stump traps were deployed at the same time as the emergence traps. Three diameter classes were used and distributed between both ponderosa pine and white fir. The diameter classes were 20-24.5 cm, 29.5-30.5 cm, and 35.5-38 cm. Similar to the log emergence traps, 3 decay classes were selected: 1) xylem hard and bark tightly attached; 2) bark beginning to separate; 3) bark beginning to fall away and xylem becoming soft. Each combination was replicated three times resulting in 54 stumps being studied each of 2 years. At the beginning of each year the plastic buckets were placed over a stump, and dirt was shoveled around the base to seal and secure the bucket from being wind blown.

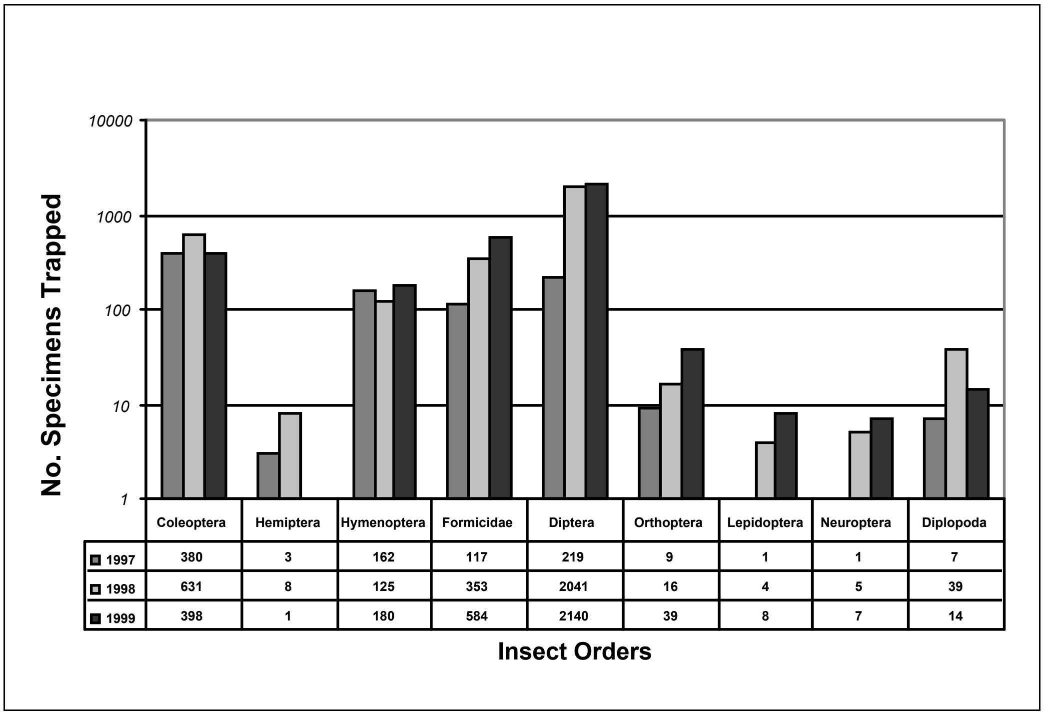
Results and Discussion

After trapping on such a large scale for 3 years, a tremendous amount of data has been gathered. The job of analyzing all of this data is ongoing. The purpose of this paper is not a rigorous analysis in detail of this study. Instead, our purpose is to summarize our findings by highlighting interesting trends indicated by the numbers of insects in broad taxonomic categories. Only the data from the emergence traps placed on logs will be considered in this paper. Samples were sorted and counted, then categorized at the ordinal level. We have identified most of the Coleoptera to the family level; some beetles were further identified to genus. We are currently working on species level identifications of these families. Finer taxonomic distinctions are beginning to show subtle differences in the faunal composition of each decay class and between tree species.

Log Emergence Traps

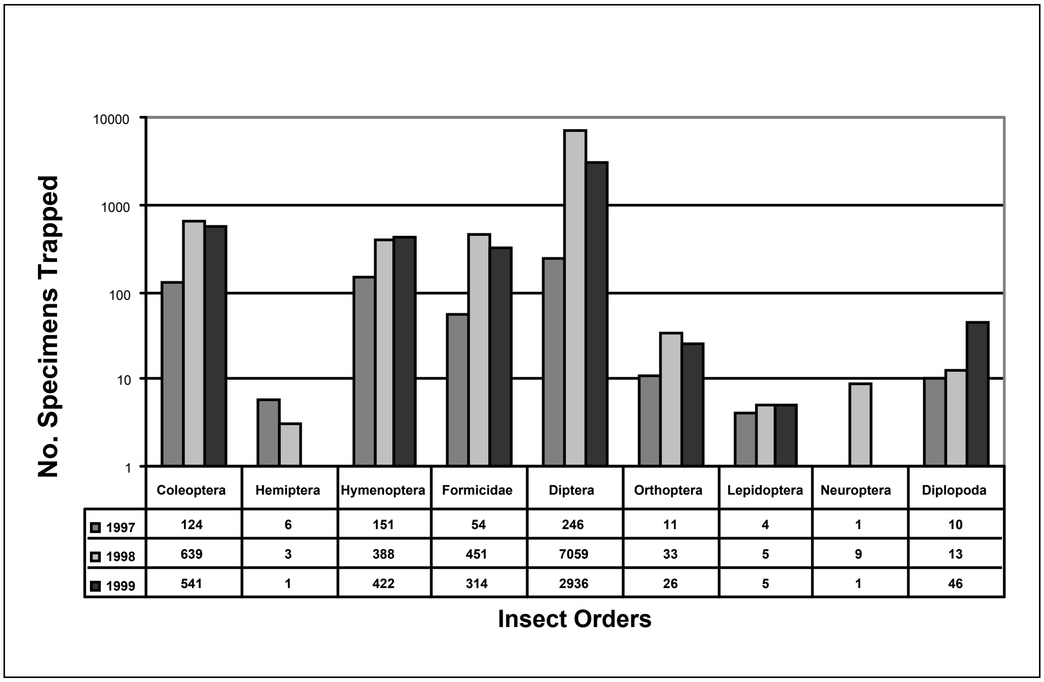
The log emergence traps were quite successful in capturing emerging insects. We have been satisfied with the design despite some persistent difficulties that seem to come with any field study. The biggest obstacle has been coping with the small mammal population, which naturally finds this new resource interesting, if not accommodating. Chipmunks (*Tamias* spp.), mice and voles (*Peromyscus* and *Microtus* spp.), shrews (*Sorex* spp.), and squirrels (*Spermophilus* spp.) have all found some use of the traps across both log species and all decay classes, to our constant frustration. Many attempts to keep them from damaging the traps have been, at best, only partially successful. We have become resigned to accepting some level of damage and dealing with it during each sample interval. This has surely influenced the results to some degree, mostly by allowing insects to escape collection due to the physical damage to the trap. With the large number of traps deployed (1998, 1999), our sample size should be able to account for this effect.

a



	Coleoptera	Hemiptera	Hymenoptera	Formicidae	Diptera	Orthoptera	Lepidoptera	Neuroptera	Diplopoda
1997	380	3	162	117	219	9	1	1	7
1998	631	8	125	353	2041	16	4	5	39
1999	398	1	180	584	2140	39	8	7	14

b

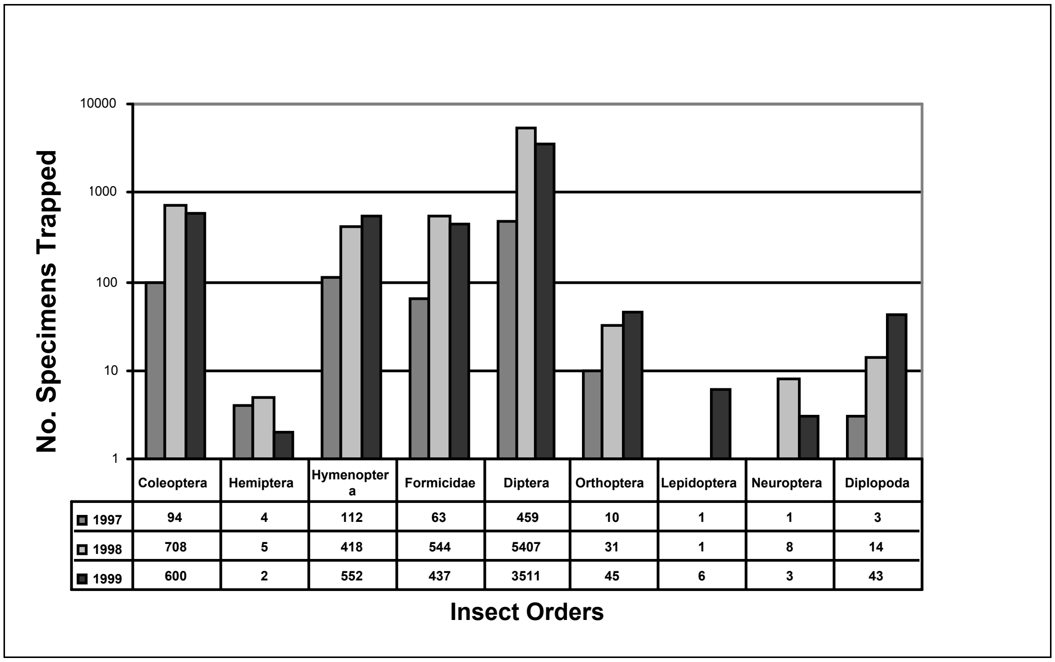


	Coleoptera	Hemiptera	Hymenoptera	Formicidae	Diptera	Orthoptera	Lepidoptera	Neuroptera	Diplopoda
1997	124	6	151	54	246	11	4	1	10
1998	639	3	388	451	7059	33	5	9	13
1999	541	1	422	314	2936	26	5	1	46

(Figure 1 continued on next page)

(Figure 1 continued)

C



	Coleoptera	Hemiptera	Hymenoptera	Formicidae	Diptera	Orthoptera	Lepidoptera	Neuroptera	Diplopoda
▨ 1997	94	4	112	63	459	10	1	1	3
□ 1998	708	5	418	544	5407	31	1	8	14
■ 1999	600	2	552	437	3511	45	6	3	43

Figure 1—Total number of insects from taxa emerging from ponderosa pine logs by decay class and year (logarithmic scale). a = decay class 1, b = decay class 2, c = decay class 3.

In reviewing the summary data *(figs. 1a-c)* from the collar traps, several patterns are evident. First, for those insects emerging from ponderosa pine, there is a remarkable similarity in the abundance of each insect order emerging from logs in all three decay classes. This holds true for both white fir and ponderosa pine. Note that the logarithmic scale was used because of the large quantities of Diptera and much smaller quantities of many other orders. The Family Formicidae in the Order Hymenoptera, is treated separately from other Hymenoptera throughout the taxonomic analysis of the data due to the large numbers captured in the emergence traps. Second, the major insect taxa in this habitat are the Diptera, Coleoptera, Formicidae, and other Hymenoptera. Third, there is little difference in the number of representatives from the higher-level taxonomic groups between each tree species. This is not too surprising given that the similarity of the resource should attract members of the same guild. However, we do expect to see increasing differences in the composition of each guild at finer levels of taxonomy. Biochemical differences in the tissues of these two tree species will likely select for organisms specifically adapted to exploiting the respective resource. This is especially true at early stages of decomposition when the presence of various defensive compounds (terpenes and phenolics) is at its greatest.

The relative abundance of some taxa differed between tree species at each decay class *(table 1)*. The most striking difference is with both tree species within decay class one, where the primary and secondary beetles (*Dendroctonus* in *Pinus* and *Pseudohylesinus* in *Abies)* are rated as abundant, but are absent in the other two decay classes. The other interesting difference is that weevils (Family Curculionidae) in decay class two of ponderosa pine are abundant, yet are rare or common in the other two decay classes of ponderosa pine and all three decay classes of white fir.

Table 1—*Relative abundance of taxa between tree species for each decay class collected during 1997-1999.*

Orders/Families	**WF1**[1]	**PP1**	**Difference**[2]	**WF2**	**PP2**	**Difference**	**WF3**	**PP3**	**Difference**
Coleoptera									
Dendroctonus	N[3]	A	XX[4]	N	N		N	N	
Pseudohyles.	A	R	XX	N	N		N	N	
Hylur./ Hylast.	R	R	X	R	R		R	R	
Gnathotricus	A	C	X	R	N	X	N	N	
Ptiliidae	C	R	X	C	R	X	C	C	
Cantharidae	R	R		R	C	X	R	R	
Cerambycidae	R	R		C	C		R	R	
Buprestidae	R	R		R	R		R	R	
Histeridae	C	R	X	C	R	X	R	R	
Staphylinidae	A	A		A	A		A	A	
Carabidae	C	C		C	C		C	C	
Curculionidae	C	C		R	A	XX	C	C	
Elateridae	C	C		C	C		C	C	
Tenebrionidae	C	C		R	R		C	R	X
Throscidae	C	C		C	C		C	C	
Leiodidae	C	C		C	C		C	A	X
Leptodiridae	C	R	X	R	C	X	R	C	X
Pselaphidae	R	R		R	R		R	R	
Nitidulidae	R	C	X	C	C		C	C	
Melyridae	R	R		R	R		R	R	
Melandryidae	R	C	X	C	C		R	C	X
Mycetophagidae	R	R		R	R		R	R	
Other Orders	A	C	X	C	C		C	C	
Hemiptera	R	R		R	R		R	R	
Hymenoptera	A	A		A	A		A	A	
Formicidae	A	A		A	A		A	A	
Diptera	A	A		A	A		A	A	
Orthoptera	C	C		C	C		C	C	
Lepidoptera	R	R		R	R		R	R	
Neuroptera	R	R		R	R		R	R	
Diplopoda	C	C		C	C		C	C	
Differences			12			7			4

[1] WF = White fir, PP = Ponderosa pine, 1, 2, and 3 are decay stages

[2] Difference denotes the change in relative abundance between each decay class

[3] Abundance categories: N = none, R = rare 1-25, C = common 26-150, A = abundant >150

[4] X = a change of 1 category; XX = a change of more than one category.

The numbers of Diptera emerging from all of the logs was surprising. Finer taxonomic analysis has not been done on these, but we suspect most belong to fungivorous taxa. The number of Diptera collected from logs over 3 years illustrates the large annual fluctuation in populations *(tables 2a-2b)*. We believe these likely are a result of weather differences. Relative to 1999, in 1998 there were many more dipterans emerging from all of the logs, except decay class 1 of ponderosa pine *(table 3)*. There appears to be more dipteran use of ponderosa pine compared to fir. In 1999, this difference is seen in all 3 decay classes, with ponderosa pine having considerably higher numbers of dipterans in each case. The 1998 data shows a clear difference in class 2, a less substantial difference in class 3, and a reversal in class 1.

Table 2a—*Collections from each decay class of log emergence traps in* Pinus ponderosa*, 1997-1999.*

Order[1]/	***Pinus ponderosa* Class 1**				***Pinus ponderosa* Class 2**				***Pinus ponderosa* Class 3**			
Family	**97**	**98**	**99**	**Total**	**97**	**98**	**99**	**Total**	**97**	**98**	**99**	**Total**
Diplopoda	7	39	14	60	10	13	46	69	3	14	43	60
Hemiptera	3	8	0	11	6	3	1	10	4	5	2	11
Hymenoptera	162	125	180	467	151	388	422	961	112	418	552	1,082
Formicidae	117	353	584	1,054	54	451	314	819	63	544	437	1,044
Diptera	219	2,041	2,140	4,400	246	7,059	2,936	10,241	459	5,407	3,511	9,377
Orthoptera	9	16	39	64	11	33	26	70	10	31	45	86
Lepidoptera	0	4	8	12	4	5	5	14	1	0	6	7
Neuroptera	0	5	7	12	0	9	0	9	0	8	3	11
Coleoptera	380	631	398	1,409	124	639	541	1,304	94	708	600	1,402
Scolytidae	209	165	0	374	2	0	0	2	0	9	0	9
Ptiliidae		5	4	9		10	2	12		81	13	94
Cantharidae	0	0	15	15	0	1	26	27	0	5	9	14
Cerambycidae	7	10	6	23	3	15	11	29	0	1	6	7
Buprestidae	0	2	0	2	1	0	3	4	0	1	0	1
Histeridae	2	8	2	12	0	1	2	3	2	5	5	12
Staphylinidae	61	130	94	285	10	140	78	228	15	166	130	311
Carabidae	1	40	23	64	9	28	36	73	4	72	45	121
Curculionidae	16	53	11	80	37	149	103	289	10	78	5	93
Elateridae	28	61	55	144	32	70	48	150	15	55	63	133
Tenebrionidae	1	15	26	42	0	1	11	12	1	4	12	17
Throscidae	3	33	53	89	1	4	25	30	2	12	21	35
Leiodidae	0	25	14	39	1	49	41	91	5	99	107	211
Leptodiridae	2	1	15	18	4	10	17	31	1	25	28	54
Pselaphidae		10	4	14		6	2	8		13	3	16
Nitidulidae		22	29	51		28	25	53		7	19	26
Melyridae	4	8	5	17	2	4	2	8	0	10	1	11
Melandryidae	46	1	10	57	22	22	71	115	39	14	74	127
Mycetophagidae		0	1	1		2	2	4		2	2	4
Other		42	31	73		99	36	135		49	57	106

[1] Insect orders are bold and families are not bold.

Table 2b—*Collections from each decay class of log emergence traps in* Abies concolor*, 1997-1999.*

Order[1]/	***Abies concolor* Class 1**				***Abies concolor* Class 2**				***Abies concolor* Class 3**			
Family	**97**	**98**	**99**	**Total**	**97**	**98**	**99**	**Total**	**97**	**98**	**99**	**Total**
Diplopoda	9	21	29	59	3	9	26	38	2	13	35	50
Hemiptera	1	3	8	12	3	16	6	25	3	7	0	10
Hymenoptera*	268	264	187	719	265	229	185	679	207	278	144	629
Formicidae	145	477	402	1,024	197	596	738	1531	138	507	464	1,109
Diptera	385	3,424	1,195	5,004	218	3,791	1,853	5,862	431	4,408	1,683	6,522
Orthoptera	9	23	32	64	16	12	19	47	5	9	24	38
Lepidoptera	3	7	13	23	5	7	9	21	4	3	2	9
Neuroptera	2	2	8	12	1	4	2	7	2	2	2	6
Coleoptera	2,229	1,826	439	4,494	113	465	471	1049	145	476	264	885
Scolytidae	2,153	759	5	2,917	2	0	0	2	1	0	0	1
Ptiliidae		39	3	42		49	10	59		64	3	67
Cantharidae		6	2	8		5	12	17		14	11	25
Cerambycidae	2	1	5	8	12	7	8	27	3	1	6	10
Buprestidae	1	3	1	5	2	0	2	4	11	0	1	12
Histeridae	1	23	9	33	10	23	15	48	0	8	3	11
Staphylinidae	16	166	71	253	15	189	97	301	36	183	39	258
Carabidae	11	21	13	45	9	22	31	62	16	19	17	52
Curculionidae	4	22	2	28	5	8	2	15	6	23	5	34
Elateridae	27	39	26	92	33	18	47	98	22	34	25	81
Tenebrionidae		14	12	28	4	7	7	18	24	5	1	
Throscidae	4	46	82	132	8	7	33	48	11	13	10	34
Leiodidae	0	58	17	75	2	32	57	91	0	51	17	68
Leptodiridae	2	4	29	35	1	2	16	19	4	4	13	21
Pselaphidae		14	2	16		13	1	14		4	0	4
Nitidulidae		11	12	23		28	84	112		19	84	103
Melyridae	0	3	7	10	0	1	5	6	0	4	3	7
Melandryidae		4	5	9		5	25	30		1	3	4
Mycetophagidae		0	1	1		3	2	5		1	2	3
Other	6	593	135	734	10	46	17	73	11	28	21	60

[1] Insect orders are bold and families are not bold.

Table 3—*Diptera from log emergence collar traps from 1997-1999.*

Year	**Decay class**	**24-Jun**	**7-Jul**	**21-Jul**	**4-Aug**	**19-Aug**	**3-Sep**	**16-Sep**	**Class Totals**
Pinus ponderosa									
	1	21	21	38	27	48	40	24	219
1997	2	21	39	24	45	54	44	19	246
	3	106	88	64	101	34	48	18	459
	1		305	279	335	455	667	194	2,041
1998	2		2,984	1,247	720	1,374	734	404	7,059
	3		791	1,745	892	1,084	895	341	5,407
	1		758	427	104	288	208	355	2,140
1999	2		997	455	283	441	290	470	2,936
	3		1,027	518	494	564	451	457	3,511

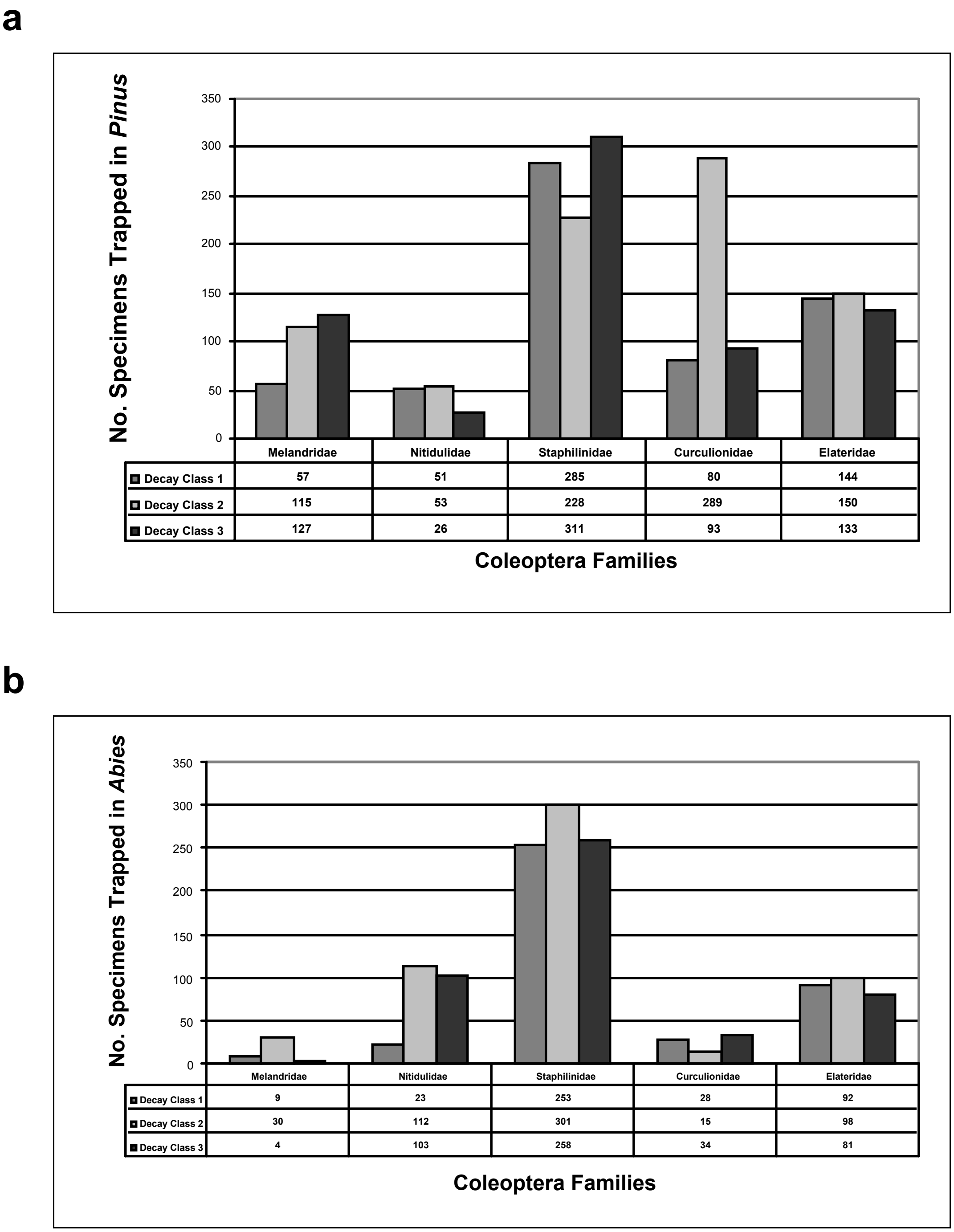
Year	Decay class	24-Jun	7-Jul	21-Jul	4-Aug	19-Aug	3-Sep	16-Sep	Class Totals
Abies concolor									
1997	1	86	45	21	51	40	110	32	385
	2	43	14	33	35	35	43	15	218
	3	35	44	144	114	26	53	15	431
1998	1		842	632	942	532	476	327	3,424
	2		848	706	694	1,034	509	283	3,791
	3		1,327	1,230	647	701	503	268	4,408
1999	1		305	254	133	182	113	208	1,195
	2		397	463	174	358	264	197	1,853
	3		454	290	159	279	207	294	1,683

Beetles, ants, and termites are commonly associated with woody material on the forest floor. Surprisingly, there were no termites collected from stumps or logs. The sample size was increased after the first year from 9 to 54 logs; yet even with the larger sample size, termites were still absent from the collections in 1998 and 1999. Collections from the pane traps indicated that the termites, *Zootermopsis nevadensis* were flying in the area (1998 data), yet none were captured in emergence traps. Perhaps the degree of decay of the logs and stumps was not advanced to the degree that mature, alate-producing colonies inhabited the logs. Furthermore, *Zootermopsis* colonies are much more common in ponderosa pine that co-occurs with white fir (Thorne and others 1993).

Hymenopterans were always abundant in the log and stump collections; most of these were Formicidae *(tables 2a-2b).* The majority of these ants were *Camponotus* spp. foragers, which were probably attempting to remove the insects in the collection jars. Occasionally, large flights of alates were collected from the stump traps, usually toward the end of summer. There were substantial numbers of other hymenopterans emerging from the logs. These consisted largely of members of the superfamilies Ichneumonoidea and Chalcidoidea and were probably parasitoids of the numerous Diptera and Coleoptera inhabiting the decomposing logs.

The abundance of Coleoptera families collected from logs of *Abies* and *Pinus* differed *(fig. 2).* Several of the commonly collected families of Coleoptera are used to illustrate distinctions in the faunal composition of these two species of trees. In addition, decay classes produced different capture rates for some families. The most striking is in the Curculionidae, which are much more abundant in each decay class of the pine compared to fir. Within the pine, decay class 2 has considerably more (289 >> 80, 93) curculionids than classes 1 and 3. This also appears to be the case for Melandryidae.

Among the Coleoptera emerging from the logs, the biggest surprise was the scarcity of the classic wood-boring beetles, Cerambycidae and Buprestidae. In ponderosa pine, the most cerambycids were collected from decay classes 1 and 2 where there were 3-year totals of 23 and 29 beetles, respectively *(table 2a).*



	Melandridae	Nitidulidae	Staphilinidae	Curculionidae	Elateridae
▨ Decay Class 1	57	51	285	80	144
☐ Decay Class 2	115	53	228	289	150
■ Decay Class 3	127	26	311	93	133

	Melandridae	Nitidulidae	Staphilinidae	Curculionidae	Elateridae
▨ Decay Class 1	9	23	253	28	92
☐ Decay Class 2	30	112	301	15	98
■ Decay Class 3	4	103	258	34	81

Figure 2—Total number of beetles collected from (a) ponderosa pine and (b) white fir for selected families of Coleoptera in each of three decay classes over 3 years.

Conclusions

We had some difficulty with the system used to classify the logs based on decay. The criteria can be quite subjective and making clear distinctions between classes 2 and 3 was sometimes difficult. This reflects our application of an artificial categorization scheme on a process that operates as a continuum. That is, the classes do not delineate distinct units in nature. Logs and stumps, at a stage in the decay process near a class break, are ambiguously assigned. A less subjective classification system would be useful. Perhaps an instrument could be developed that designates the stage of decay based on the softness of the wood.

There is still a considerable amount of data to be assembled, summarized, and analyzed. In addition to the obvious analysis, concerning biological diversity—especially at fine taxonomic levels—there remains analysis of the flight periodicity of the various orders. Fortunately, we collected the log, stump, and pane traps on a regular basis from approximately June until the end of September of each year. This will allow us to describe the periods of flight activity for each of the major groups. This data could be valuable to other researchers who want to investigate these groups in more detail.

Finally, the decay of CWD is a long and complex process that involves different groups of organisms playing different roles. The process is set on a trajectory from the time a tree is killed, often by the primary beetles, to the time the chemical constituents are returned to the soil as soil nutrient. In addition to the role that various insect groups play in the decay process, it should be emphasized that they also function as prey items to various vertebrate organisms. The important role of insects as prey is poorly understood and should gain more attention.

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A Preliminary Study of Ant Diversity and of Ant Dependence on Dead Wood in Central Interior British Columbia[1]

B. Staffan Lindgren[2] and A. M. MacIsaac[2]

Abstract

Nineteen species of ants in three subfamilies and seven genera were found during a preliminary survey near Prince George, British Columbia. Ant diversity was low to moderate, with up to 7 species collected within areas of less than 1 ha in size. Wood was the preferred nest substrate for the majority of species, with 12 of the species utilizing wood in more than 69 percent of the collections. The nests of three to four species frequently shared logs or stumps.

Introduction

Ants are known to be ecologically significant invertebrates in many ecosystems (Hölldobler and Wilson 1990). They positively affect physical and chemical soil properties, plant and animal distribution, and forest health. Some species (e.g., carpenter ants [*Camponotus* spp.]) attain direct pest status because they may cause serious structural damage in buildings. Other species invade homes, and some cause indirect damage to plants by tending aphids and scale insects. Ants serve as important food for many vertebrates, including woodpeckers (Torgersen and Bull 1995) and both grizzly and black bears (Kansas and others 1989, Raine and Kansas 1990). For example, Raine and Kansas (1990) found that "The ant season was found to occur from mid-June to mid- to late July, when berries began to ripen. Ants and ant larvae were the main food items observed to be eaten by bears during this season. Bears searched for ants in old logs and under stones" (p. 299). In terms of biomass, ants often dominate in warm temperate and tropical ecosystems, but become increasingly less important with increasing latitude. For example, Francoeur (1983) found only four species at the tree line in Quebec.

Ants have been poorly studied in the sub-boreal forests of central British Columbia (BC). Few collections are available, and the species that occur there can only be deduced by puzzling together data from adjacent regions. In a recent synthesis of what is known about the ant fauna in BC (Naumann and others 1999), only one species, *Formica podzolica* Francoeur, is represented by collections near Prince George *(table 1),* where our study is conducted. Francoeur (1997) found 19 species in the Yukon, the majority of which are also present in BC. It is also possible

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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that transcontinental species not listed in *table 1*, but listed by Francoeur (1997) as being present in the Yukon, occur in north-central BC. However, no records exist. The number of species in the north-central part of BC is uncertain, because Buckell (1932), from which most of the northern information in *table 1* is derived, does not specify locales. Instead, he indicates wide geographic regions, *e.g.*, the Chilcotin, which spans several biogeoclimatic zones (Meidinger and Pojar 1991). In other words, many ant species that occur in the southern parts of the Chilcotin or Cariboo regions are unlikely to occur in the Prince George area.

Table 1—*Ant species listed as occurring in north central British Columbia, or that can reasonably be expected to occur there. Data based on Naumann and others (1999) and Francoeur (1997).*

Subfamily Species	Locality/range	Reference
Myrmicinae		
Myrmica alaskensis	Cordillera	Francoeur 1983
Myrmica incompleta	Lac LaHache	RBCM[1]
Myrmica lobicornis	Arizona-Alaska	Smith 1979
Myrmica brevispinosa	Chilcotin, Cariboo,	Buckell 1932
	Alaska	Nielsen 1987
Aphaenogaster subterranea	Chilcotin	Buckell 1932
Solenopsis molesta	Throughout BC	Buckell 1932
Leptothorax muscorum	Arizona-Alaska	Smith 1979
Leptothorax retractus	Yukon	Francoeur 1997
Dolichoderinae		
Tapinoma sessile	Chilcotin	Buckell 1932
Formicinae		
Camponotus herculeanus	Chilcotin	Buckell 1932
Camponotus modoc	Chilcotin	Buckell 1932
Camponotus noveboracensis	Chilcotin	Buckell 1932
Camponotus vicinus	Chilcotin	Buckell 1932
Lasius alienus	70 Mile House	RBCM
Lasius flavus	Chilcotin	Buckell 1932
Lasius pallitarsis	Lac La Hache	RBCM
Formica lasioides	Chilcotin	Buckell 1932
Formica neogagates	Chilcotin	Buckell 1932
Formica fusca	Chilcotin, Cariboo	Buckell 1932
Formica neoclara	Lac LaHache	RBCM
Formica neorufibarbis	Barkerville	Buckell 1932
	Liard Hot Springs	Francoeur 1973
Formica podzolica	Prince George	UBC[2]
Formica subpolita	Chilcotin	Buckell 1932
Formica dakotensis	New Mexico-Alaska	Smith 1979
Formica obscuripes	Chilcotin	Buckell 1932
Formica oreas	Chilcotin	Buckell 1932
Formica aserva	Lac LaHache	RBCM
Polyergus breviceps	Chilcotin	Buckell 1932

[1] Royal British Columbia Museum, Victoria, B.C.

[2] Spencer Museum, University of British Columbia, Vancouver, B.C.

Ants utilize various substrates for nesting, including dead wood. Hölldobler and Wilson (1994) note that ants nest preferentially under flat rocks in cooler climates, because these have low specific heat when dry, and thus heat up faster than the surrounding soil. Similarly, the large thatch mounds of many species in the *Formica rufa* group are beneficial in cold climates (Hölldobler and Wilson 1994). Wheeler and Wheeler (1986) provide a list of ants in Nevada, indicating typical nest substrates. Of 177 species, only 15 regularly utilize dead wood substrates for nesting, and another two species nest under wood or other substrates. Most nest under rocks, or build nests directly in exposed soil, which is prevalent in the drier biomes of Nevada (Wheeler and Wheeler 1986). Of the 17 species listed as utilizing wood, 10 are listed in *table 1*, i.e., they are likely to occur in central BC. Of 82 species of ants occurring in North Dakota, Wheeler and Wheeler (1963) listed 29 that nest in wood, and an additional 9 species that nest in soil under wood, i.e., almost half of the species regularly utilize wood for their nests.

In the relatively wet sub-boreal forests, typical of the area around Prince George, exposed rocks are rare but dead wood of all sizes and ages is plentiful, both in natural stands and in stands with a history of harvesting. Thus, it is reasonable to hypothesize that dead wood constitutes an important nest substrate for many ant species. The objectives of this study are: 1) to conduct a survey of ant species in the Prince George area, 2) to determine to what extent wood is utilized as a nest substrate, and if specific substrate attributes are associated with particular species of ants, and 3) to estimate ant abundance. This paper reports on preliminary findings from data collected in 1999. No formal measurements of ant abundance were made at this preliminary stage due to limitations in time and resources. Thus, ant abundance in this paper is only reported subjectively.

Materials and Methods

The study was conducted in the area around Prince George in central BC. The area is in the sub-boreal spruce biogeoclimatic zone, which is dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud) and hybrid spruce (*Picea glauca x engelmanni* (Parry) Engelmann) forests (Meidinger and Pojar 1991).

Species Survey

Ants were collected from a variety of environments, including urban sites within the city of Prince George. Since the objective was to obtain and identify as many species as possible, we included ants from traps and collections of unrelated studies conducted from 1997 to 1999 in the same area, ants from the nest survey (see below), and stray ants that were encountered. Ants were tentatively identified to species by using the keys of Francoeur (1973), Hansen and Akre (1985), Naumann and others (1999), and Wheeler and Wheeler (1963, 1977, 1986). In cases where identification to species was not possible, ants were designated a morphospecies number. Specimens were then sent to experts for identification. Dr. André Francoeur (Directeur, Centre de données sur la biodiversité du Québec, Chicoutimi, Québec) (*Myrmica, Leptothorax*) and W. B. Preston (946 McMillan Ave., Winnipeg, Manitoba) (all other genera) identified these to species.

Nest Survey

The nest survey was restricted to lodgepole pine stands at this preliminary stage of the study, but will eventually be expanded to include all forest types. Thus, collections were done in lodgepole pine stands approximately 15–100 years old located west and southwest of Prince George. Twenty to thirty worker ants were collected from nests by hand. Reproductives were collected when available. Depending on the species, individuals were picked directly from the nest, or a portion of the nest substrate was transferred to a white plastic bucket, from which the ants could be transferred to small vials containing 70 percent ethanol. The most aggressive species were transferred again by tipping the bucket and directing the ants to run out over the edge into a small container containing soapy water, from which they could easily be collected after a few minutes. Each nest was assigned a field number, and in the majority of cases the substrate was photographed. The nest substrate was measured, and the integrity and general condition of the wood noted.

Results and Discussion

Species Survey

Species identification of ants is difficult because of a lack of reference collections and the fact that most of the available keys are either out of print and unavailable (e.g., Creighton 1950), or are restricted to the ant fauna of specific regions (Wheeler and Wheeler 1963, 1986). A manuscript version of the key in Naumann and others 1999, which is specific to ants in BC, was valuable in that distribution records for the province could be consulted *(table 1).* However, since most collections have been done in southern BC, even these records were of limited use. Existing keys for the genera *Myrmica* and *Leptothorax* (Subfamily Myrmicinae) are unreliable, and these genera are under revision (Francoeur 1997). The names used follow Bolton (1995).

Based on our preliminary survey, we found 19 species of ants in 7 genera that occur in the area *(table 2).* Of these *Manica invidia* Wheeler (= *mutica* Emery), *Myrmica fracticornis* Forel (= *detritinodis* Emery), *Lasius subumbratus* Viereck, *Formica hewitti* Wheeler, *F. argentea* Wheeler, and *F. obscuriventris* Mayr were not expected to occur in the area surveyed based on available information *(table 1).* In other words, 31.6 percent of the species we found in this preliminary survey had not been collected previously in north central British Columbia. Diversity can be moderate locally, e.g., Lindgren (personal observation) has found seven species occurring in and around the yard of his personal residence (an area of about 0.25 ha) in the city of Prince George. Normally, we found four to six species in any one area, often with three or more species sharing nest resources, or at least nesting in close proximity to each other.

Nest Survey

Subfamily Myrmicinae

We found that wood was utilized by ants to a high degree for nesting. In an unrelated study in 1998, we found that small nests of *Myrmica incompleta* (Provancher), *M. alaskensis* Wheeler and *M. fracticornis* Forel were common under the bark of lodgepole pine stumps, which were only 12 months old and still had active bark beetle infestations. Of 24 records of these three *Myrmica* species located in this study, more than 75 percent were found in wood (*table 2*). In most cases they were found in the mature forest.

Table 2—*Species list of ants collected in the Prince George area, May–August, 1999, and information of their use and characteristics of wood for nesting.*

Subfamily **Species**	**Use of wood (pct)**	**Length range (cm)**	**Diameter range (cm)**	**Predominant consistency of wood**	**N**
Myrmicinae					
Myrmica alaskensis	100	17-900	10-59	Rotten	6
Myrmica brevispinosa	25	38	10	Rotten	4
Myrmica fracticornis	83.3	3-120	4-8	Very rotten	6
Myrmica incompleta	75	15-1300	10-50	Rotten	12
Manica invidia	0	–	–	–	1
Leptothorax muscorum	91.7	10-1300	5-25	Rotten	12
Dolichoderinae					
Tapinoma sessile	50	17-700	10-59	Solid	6
Formicinae					
Camponotus herculeanus	100	50-800	10-50	Solid	10
Camponotus modoc	100	50	500	Solid	1
Lasius pallitarsis	73.3	15-350	8-53	Very rotten	15
Lasius subumbratus	0	–	–	–	1
Formica lasioides	n/a	–	–	–	1
Formica obscuripes	0[1]	–	–	–	3
Formica obscuriventris	50	300	30	Rotten	2
Formica argentea	50	20-100	16-46	Rotten	10
Formica fusca	100	33-150	20-77	Variable	3
Formica hewitti	100	36	6	Rotten	2[2]
Formica neorufibarbis	100	250	15	Heartrot	1
Formica aserva	91.7	10-900	10-77	Rotten	12

[1] Pine needle thatch mounds.

[2] Measurement missing from a log.

In 11 of the 24 records, the nests were found in logs also occupied by other ant species, and in 6 of those records these were nests of *Formica* spp. or *Camponotus herculeanus* (Linnaeus). One nest of *Myrmica brevispinosa* Wheeler was found in wood in an open area at the edge of a ca. 15-year old stand of lodgepole pine, but this species appears to be more likely to nest in the soil. We never found this species in the mature forest.

Nests of *Leptothorax muscorum* Nylander (=*canadensis* Provancher) were particularly common in wood occupied by other species. The nests of these minute ants were found in a variety of situations, but were often close to the surface of the wood, where it was dry and relatively firm. Nests were also found in very small pieces (10 x 15 cm in one case) of wood on the ground, where other species were not present. Nests of these ants were easily found by looking for fine excavating dust, which would accumulate under or in crevices on the wood containing an active nest.

Subfamily Formicinae

Camponotus herculeanus was the only species of carpenter ant we encountered in the pine forests, and it was always found in relatively large pieces of wood, i.e., stumps or down logs. This is similar to what was found for *C. modoc* Wheeler in Oregon (Torgersen and Bull 1995). Although we found evidence of *C. herculeanus* nests in standing live trees, we did not collect from these, since collecting would have required cutting the trees down. The nests were usually not evident until the wood was broken open, since carpenter ants frequently pack excavated wood in tunnels and galleries (Sanders 1964). Majors of *C. herculeanus* are quite impressive in size, but this is a very timid species. When a nest was opened, the ants would rush about trying to save their brood, but were extremely reluctant to attack. In fact, groups of workers were frequently found cowering in chambers as they tried to escape the intruders. *C. herculeanus* occurred mainly in shaded locations, e.g., in mature stands. Unlike *C. modoc*, which Torgersen and Bull (1995) found to apparently avoid lodgepole pine, *C. herculeanus* used this species frequently. *C. modoc* was found during the species survey in a Douglas-fir stand, situated on the ridge at the top of a south-facing slope, but was never encountered elsewhere.

In exposed areas, carpenter ants were replaced by *Formica aserva* Forel (=*subnuda* Emery). These aggressive ants were particularly prevalent in stumps, where their presence was usually quite evident due to the bustling activity of the ants themselves, excavating dust, and accumulations of thatching materials around the base of the nest. Disturbance of the nest brought about an immediate response of a large numbers of ants, which never hesitated to attack. Based on our preliminary observations, these ants favored low stumps and down logs with limited decay. *F. aserva* workers were at times observed carrying prey or tending aphids. It is the ants in the *Formica rufa* and *F. sanguinea* groups, along with the carpenter ants, that may contain the majority of potentially beneficial ants (Youngs and Campbell 1984), both by physically breaking down wood and as predators (although see Sanders and Pang 1992).

In one mature lodgepole pine stand within the city of Prince George, we found numerous large thatch mounds of *Formica obscuripes* Forel. The nests appeared to be polycalic, i.e., small accessory thatch mounds were in close proximity to the two large mounds from which we collected the ants. The largest dome had a base of 200 x 250 cm and was about 100 cm tall. This attractive species was also extremely aggressive when defending nests. We could not determine if nests were initiated in wood, since this would have meant destroying the mounds

Ants in the *Formica fusca* group, primarily *F. argentea, F. hewitti,* and *F. fusca* Linnaeus also commonly used wood *(table 2). F. argentea* were found in soil nests in seven of ten cases. These soil mounds can be quite large, e.g., we found one nest covering more than 4 m^2 with a height of about 30 cm at its apex. Thus, this species is potentially important in terms of soil processes in the area surveyed, as are other species in the *F. fusca* group (Wiken and others 1976). In one of two cases where we dug up the nest, we found a rotten piece of wood at the center of a nest, indicating that the nest had been founded in wood. Both *F. hewitti,* and *F. fusca* nests were found in wood. These species were relatively aggressive, but in small nests workers usually tried to hide, rather than defend the nest.

Lasius pallitarsis (Provancher) was the only species in this genus encountered during the nest survey. In forest environments we found this small species in very wet, rotten wood more or less buried in the soil. Small-diameter stumps were a particularly favored habitat. In several cases, the nest substrate was shared with *Myrmica* species. Nests were found in mature, as well as young pine forests, but we also found nests of these versatile ants under rocks and other objects in open fields. This is consistent with the information in Naumann and others 1999.

Subfamily Dolichoderinae

The only species in this genus was the ubiquitous *Tapinoma sessile* (Say). This diminutive, but aggressive, species showed no preference for nest substrate, consistent with its ability to inhabit virtually any habitat (Wheeler and Wheeler 1963).

Abundance

Although no quantitative assessment of ant abundance was made, we judged ants to be numerous locally, particularly in open areas. Thus, they may be presumed to be an important component of the arthropod fauna in the area studied. The relative abundance of most of the species encountered in our study appeared to be favored by the presence of woody debris. A quantitative assessment of the relationship between the abundance of ants and woody debris needs to be done to establish whether or not this is true.

Conclusion

Because little is known about the ecology of most of the species present in the sub-boreal forests of interior BC, it is difficult to assess in what ways ants contribute to ecosystem function. Some species of ants are highly significant as predators of forest defoliators, and as a primary food source for woodpeckers (Torgersen and Bull 1995). Further studies on the ecological roles of ants in sub-boreal forests are needed to determine their relative importance. It is clear from our preliminary study that woody debris constitutes an important habitat component for ants. For some species, the availability of woody nest substrates may limit nest founding success, and ultimately populations of ants. Additional information is required on the ecological significance of ants in sub-boreal forests, and the characteristics of wood associated with the nests of different species. Such information would ensure that beneficial species of ants could be promoted by providing suitable nest habitats in a manner similar to what is being done for cavity nesting birds. We intend to continue with the species inventory, and to conduct research on the ecological roles of ants in sub-boreal forests.

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Effects of Ecosystem Restoration Treatments on Cavity-nesting Birds, Their Habitat, and Their Insectivorous Prey in Fire-maintained Forests of Southeastern British Columbia[1]

Marlene Machmer[2]

Abstract

Long-term fire suppression and cessation of aboriginal burning has resulted in forest ingrowth and associated structural and functional changes to dry, fire-maintained forests of southeastern British Columbia. In this experimental study, effects of ecosystem restoration treatments (prescribed fire, partial harvesting, prescribed fire and partial harvesting, and untreated controls) on cavity-nesting birds, their habitat, and their insectivorous prey were investigated. Pre- and post-treatment data on the nesting density of cavity-nesters, the availability of wildlife trees, the foraging intensity of woodpeckers, and the relative abundance and species diversity of insects each breeding season were gathered, beginning in 1996. Preliminary results (1996 to 1998) indicate that harvested treatments were associated with a decline in the nesting density and species richness of cavity nesters over the short term; snag densities decreased in harvested and burned treatments; the number of trees per hectare with fresh woodpecker foraging sign did not differ significantly comparing pre- and post-treatment; and large increases in the relative abundance of selected insect species in some families were apparent in the treated units. Insect response was most pronounced in the burn only treatment, followed by the harvest and burn, and the harvest only treatments. Management implications for future ecosystem restoration efforts are discussed.

Introduction

In the Rocky Mountain Trench and adjoining side valleys of southeastern British Columbia, an estimated 250,000 ha of land within the ponderosa pine (PP) and interior Douglas-fir (IDF) biogeoclimatic zones is classified as Natural Disturbance Type 4 (NDT4). Before 1900, these forests were characterized by "frequent, stand-maintaining fires" resulting in open park-like conditions with widely-spaced large old trees, sparse regeneration, and low incidence of insects and diseases (Arno and others 1995, Covington and Moore 1994, Daigle 1996, Gayton 1996). Systematic and long-term fire suppression and cessation of aboriginal burning has eliminated fire from these forests. This has stimulated forest ingrowth and encroachment, with associated reductions in ungulate forage quantity and quality, increased risk of stand

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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replacement fires, and major forest insect and disease outbreaks. Recent operational trials have used mechanical treatments (e.g., partial cutting, slashing pruning) and prescribed fire in an attempt to restore the fire-maintained character of these forests (Gayton and others 1995, Hawe and DeLong 1998, White 1997). Once stands have been thinned and fuels have cured, prescribed burning can be carried without the risk of catastrophic fire, while providing some revenue from sawlogs and pulp. Effects of restoration treatments on wildlife communities have not been well documented in an experimental context (Finch and others 1997, Saab and Dudley 1997).

This study focuses on cavity-nesting birds—birds that are dependent on standing dead and defective live trees for nesting, roosting and feeding (Bull and others 1997, Raphael and White 1984, Steeger and others 1996). In dry, fire-maintained forests, the proportion of cavity-nesting species is comparatively high relative to other forest-dwelling vertebrates (Bunnell 1995). Burns create fire-scorched or killed trees, which are attractive to a host of wood, bark, and cambium-dwelling insects (Amman and Ryan 1991, Fellin 1980, Furniss and Carolin 1977, Samuelsson and others 1994). These insects form the prey base for many cavity-nesting species (Machmer and Steeger 1995). I hypothesized that the temporal and spatial occurrence of burns would have a strong influence on the population dynamics of this wildlife guild.

The objectives of this study are to investigate the individual and combined effects of ecosystem restoration treatments on the nesting abundance and species richness of cavity nesters, the availability of wildlife tree habitat, the foraging intensity of woodpeckers, and the relative abundance and species richness of wood-associated insects. In this paper, preliminary (1996 to 1998) results are reported, and some management implications for future restoration treatments are discussed.

Study Area and Design

The study is being conducted in the Ta Ta Creek range unit (49°46’N, 115°46’W) located 45 km north of Cranbrook in the Rocky Mountain Trench of southeastern British Columbia. The study area is in a flat valley bottom (850 to 900 meter elevation) and consists of moderately dense to semi-open multi-storied stands of 90- to 100-year-old Douglas-fir *(Pseudotsuga menziesii)* and ponderosa pine *(Pinus ponderosa)*. Small pockets of lodgepole pine *(P. contorta)* and trembling aspen *(Populus tremuloides)* are found in draws and wetter sites. Fire has been excluded from these for an estimated 60 years.

Three treatments (25 ha burn only; 40 ha harvest and burn; and 40 ha harvest only) and two control areas (one located adjacent to and a second located 3.5 km away from the treatment units) were tested without replication during operational trials. A uniform “shelterwood with reserves” silvicultural system was used for harvest treatments with the following objectives for post-harvest target densities: 26-36 stems ha^{-1} (sph) of layer 1a (20-65 cm dbh) healthy, well-formed veteran/dominant ponderosa pine and Douglas-fir; 5-20 sph of layer 1b (15-20 cm dbh) ponderosa pine and Douglas-fir; 10-20 sph of layer 2 (10-15 cm dbh) ponderosa pine and Douglas-fir; and 50-60 sph of layer 3 (3-5 cm dbh) ponderosa pine. Post-harvest slashing of small sub-merchantable stems was conducted in the harvest and burn treatment to ensure sufficient fuel to carry the fire. Burning treatments involved low-intensity prescribed fire with the following specific objectives: eliminate 75 and 25 percent of trees in the < 5 and < 15 cm diameter at breast height (dbh) classes, respectively; limit mortality of trees > 30 cm dbh to < 10 percent; prune all trees to a height of 2 m; and reduce ground fuels <10 cm and > 20 cm diameter by 50-75 and 5-10 percent, respectively. Harvesting was completed in February of 1997, and burning was conducted during April of 1998. Resulting stands differed visibly in terms of large stem densities and associated stand structure: post-treatment (1999) densities of trees > 10 cm dbh averaged 160, 48 and 161 sph in the burn only, harvest and burn and harvest only treatments, respectively, while densities of smaller stems were relatively comparable among treated areas.

Methods

We established 20 ha core sampling areas in each of the five treatment units during spring of 1996. These areas were monitored pre- and post-treatment during the 1996 to 1999 breeding seasons.

Cavity Nest Inventory

From early May to late June, we systematically searched the sampling areas for the presence of cavity-nesting species (both primary cavity excavators and secondary cavity users) and cavities in trees. We considered a nest active if parents were observed incubating, tending a brood, feeding young, or if young were heard vocalizing within the cavity. Two observers visited each of the five treatment units weekly on a regular rotation for 7 weeks (70 observer-days/season). We monitored nests weekly to determine their status and fate (i.e., success or failure), and calculated cavity nest densities for each treatment, excluding pairs that failed prior to confirming incubation.

Wildlife Tree Inventory

We assessed the number and characteristics of all standing live healthy trees, dead trees, and wildlife trees (i.e., dead trees, live defective trees, and live trees with evidence of foraging sign) > 10 cm dbh in stratified random plots of 11.28 m radius before (1996) and after (1998) treatment. Tree characteristics included tree species, dbh, height, decay class (British Columbia Wildlife Tree Committee 1997), and presence of particular tree defects and disturbance agents. A total of 100 plots (20 plots per treatment unit) were sampled in late June of each year.

Woodpecker Foraging Inventory

We assessed all trees (no diameter limit) in the random plots for evidence of fresh woodpecker foraging activity before (1996) and after (1998) treatment. Freshly "woodpeckered" bark characterized by newly exposed wood was readily distinguished from old foraging sign that appears discolored. We classified foraging sign as scaling, excavations, or sapsucking. This method is conservative in that it excludes foraging that does not leave quantifiable sign, such as gleaning of insects from bark or foliage. To assist with the interpretation of foraging sign data, we made opportunistic observations on foraging woodpeckers during surveys in the sampling areas.

Insect Trapping

We used Lindgren multiple-funnel traps (baited with an ethanol-releasing device and containing a Vapona pest strip)[3] to assess the abundance and diversity of arboreal beetles and other insects likely to serve as prey items for woodpeckers and other cavity-nesting species. Four traps were suspended (between trees with collection cups at 0.5 to 1.0 meter above ground level) in each treatment unit from late April to early September. Catches were collected every 3 weeks and stored in plastic bags at -10°C. Later, insects were sorted to family, identified to species or genus, and tallied. Insect analyses are still in progress and only preliminary; 1996—1998 results are presented here.

Results

Cavity Nest Density and Species Richness

We found a total of 10 cavity-nesting species breeding in the study area: hairy *(Picoides villosus)* and pileated woodpeckers *(Dryocopus pileatus),* northern flicker *(Colaptes auratus),* white- *(Sitta carolinensis)* and red-breasted nuthatches *(S. canadensis),* black-capped *(Parus atricapillus)* and mountain chickadees (*P. gambeli*), mountain bluebird *(Sialia currucoides),* red squirrel *(Tamiasciurus hudsonicus),* and northern flying squirrel *(Glaucomys sabrinus).* Pre-treatment (1996) cavity nest densities ranged from 2 to 10 nests per 20 ha treatment unit (0.1 to 0.5 nests per ha; *fig. 1*). After harvest treatments were completed in 1997, nest densities in the harvest and burn and harvest only treatments decreased by 50 percent. Those in the burn only treatment (still untreated in 1997) increased by 50 percent, relative to pre-treatment. Nest densities in adjacent and distant controls increased and decreased respectively, during this period. After burning treatments were completed in 1998, nest densities remained 50 percent lower than pre-treatment in the harvest only, and were either comparable to or higher than pre-treatment in all other units. Of the post-treatment cavity nests found in the harvested treatments, 50 percent in the harvest only (1997 and 1998) and 33 percent in the harvest and burn (1998 only) were located in wildlife tree patch-reserves, rather than in harvested portions of the treated units. These reserves comprised only 4.2 percent of the total area harvested, yet they supported up to half the breeding cavity nesters. Although sample sizes are low and statistical comparisons are not possible due to lack of replication, these results suggest that over the short term the harvest only treatment was associated with a decrease in cavity nest densities.

Pre-treatment species richness of cavity nesters was low, ranging from two to four species per treatment unit *(fig. 2).* Following harvest in 1997, nesting species richness decreased in both harvested treatments, but remained constant in the adjacent control, and increased in the burn only and distant control. After burning was completed in April of 1998, cavity nesting species richness was 50 percent lower in the harvest only and higher in all other units, relative to pre-treatment. These trends also suggest a short term decrease in cavity-nesting species richness associated with the harvest only treatment.

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[3] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

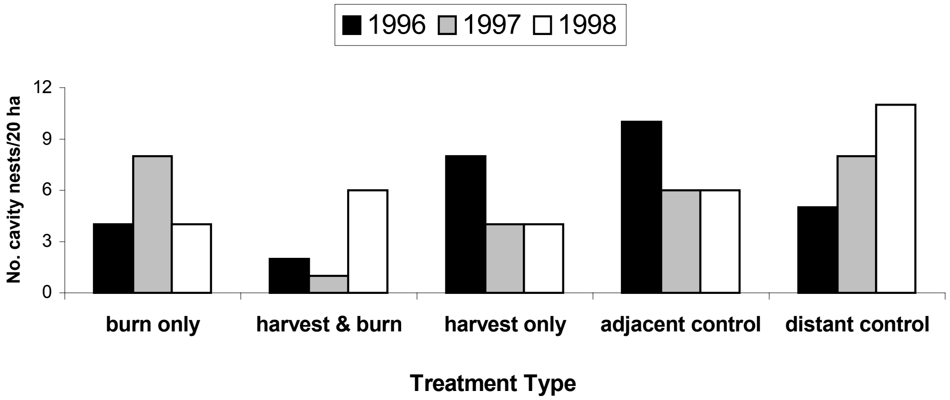

Figure 1—Number of active cavity nests per 20 ha treatment unit by year (1996 to 1998) and treatment type in the Ta Ta Creek operational trial, southeastern British Columbia. Note that 1996 was a pre-treatment, 1998 was a post-treatment year, and 1997 was pre-treatment for burning and post-treatment for harvesting activities.

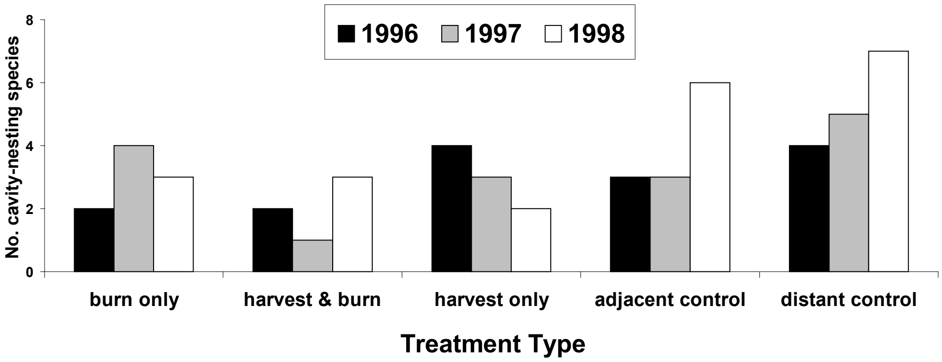

Figure 2—Number of cavity-nesting species per 20 ha treatment unit by year (1996 to1998) and treatment type in the Ta Ta Creek operational trial, southeastern British Columbia. Note that 1996 was a pre-treatment, 1998 was a post-treatment year, and 1997 was pre-treatment for burning and post-treatment for harvesting activities.

The mountain bluebird was the only species to nest in a treated area (burn only) after treatment that was not breeding there before treatment. Conversely, the northern flying squirrel and white-breasted nuthatch did not breed in treated units (harvest only and burn only, respectively) once treatments were completed, although they were nesting there before.

Availability of Wildlife Trees

The harvest and burn and harvest only treatments showed reductions in basal area of 60.6 and 66.4 percent, respectively, as determined during a companion study monitoring vegetation response to treatments (Penniket & Associates 1998). As expected, total densities of trees measuring > 10 cm dbh differed significantly between years and among treatments *(fig. 3)*. In particular, the two harvested treatments showed significant post-treatment declines (two-way Anova: F = 11.2, df = 1, $P = 0.001$ for year; F = 3.66, df = 4, $P = 0.05$ for treatment; F = 3.69, df = 4, $P = 0.006$ for treatment × year).

Snag densities ranged from 2.5 to 12.5 snags per hectare in the treatment units in 1996 compared with 0.1 to 15.0 snags per ha in 1998 *(fig. 3)*. All three treated units had lower snag densities post-treatment, i.e., decreases of 97 percent in the burn only, 98 percent in the harvest and burn and 50 percent in the harvest only, while densities in adjacent and distant controls were 48 percent lower and 50 percent higher, respectively, relative to pre-treatment. Differences among treatments and between years were not statistically significant (two-way Anova: F = 0.718, df = 4, $P < 0.581$ for treatment; F = 1.13, df = 1, $P = 0.289$ for year; F = 0.732, df = 4, $P = 0.571$ for treatment × year).

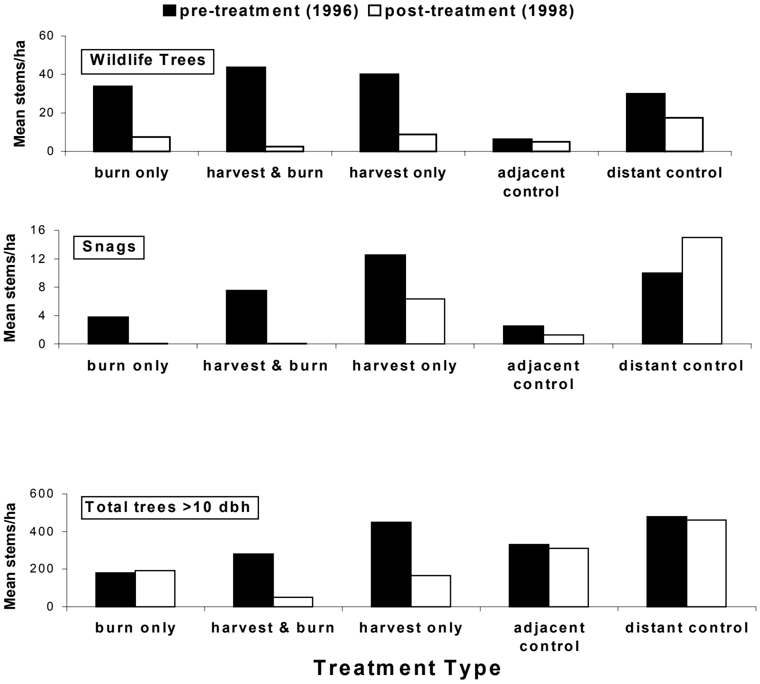

Figure 3—Densities (stems ha^{-1}) of wildlife trees, snags, and all trees (> 10 cm dbh) by treatment type in 1996 (pre-treatment) and 1998 (post-treatment).

Pre- and post-treatment, the densities of wildlife trees were significantly lower in 1998, but differences among treatments and interactions between treatment and year were not (two-way Anova: F = 20.4, df = 1, $P < 0.0001$ for year; F = 2.03, df = 4, $P = 0.092$ for treatment; F = 2.00, df = 4, $P = 0.097$ for treatment × year). The significant year-effect is related to the way wildlife trees were defined (i.e., dead trees, live defective trees, and live trees with evidence of foraging sign or other wildlife use), and reflects the significantly lower level of woodpecker foraging activity found on trees in the overall study area in 1998 (see below).

Woodpecker Foraging Intensity

Woodpecker scaling and excavations accounted for approximately 80 and 20 percent, respectively, of foraging observations in both years (81.4 scaling and 18.6 percent excavations in 1996 compared with 79.3 scaling and 20.7 percent excavations in 1998). The number of trees with fresh woodpecker foraging sign in the treatment units ranged from 5 to 22.5 trees/ha in 1996 and 2.5 to 15 trees/ha in 1998 *(fig. 4)*. Differences between years were significant; however, treatment effects and interactions between treatment and year were not (Two-way anova: $F = 4.69$, $df = 1$, $P < 0.0317$ for year; $F = 0.444$, $df = 4$, $P = 0.777$ for treatment; $F = 0.444$, $df = 4$, $P = 0.777$ for treatment × year). Woodpecker foraging activity on trees was lower in the winter, spring, and early summer preceding our June 1998 observations than in the corresponding seasons prior to 1996. These differences were not treatment related and may be linked to abiotic factors (e.g., temperature, snow pack) affecting the entire study area.

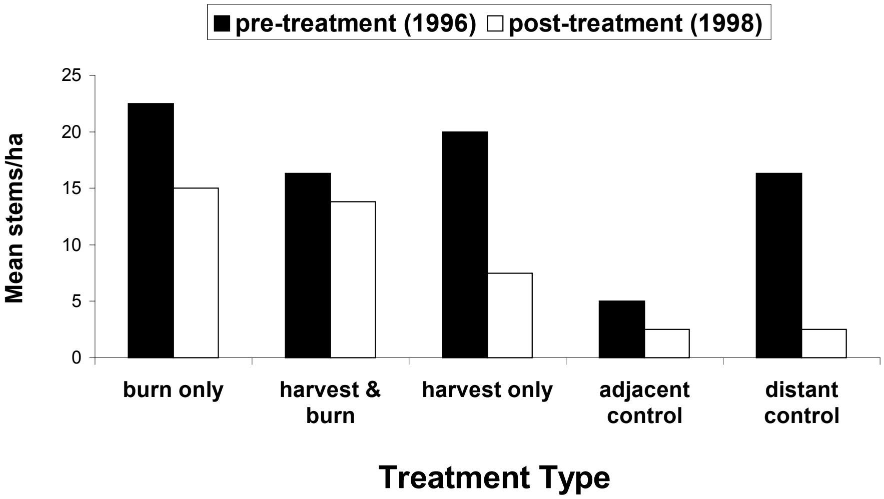

Figure 4—Density (stems ha^{-1}) of trees with fresh woodpecker foraging sign by treatment type in 1996 (pre-treatment) and 1998 (post-treatment).

Abundance and Diversity of Insects

Pre-treatment insect diversity and abundance was similar across treatment units, with a total of 1,919 individuals, 84 species, 57 genera, and 25 families represented in trap catches (Wilson 1999). After treatments were completed in 1998, 10,642 individuals representing 98 species, 68 genera, and 26 families were tallied in catches. Relative to controls, all three treated units showed large (>100 percent) post-treatment (1998) increases in abundance of selected species in the following families:

Buprestidae, Cerambycidae, Cleridae, Hymenoptera, Nitulidae, Oedemeridae, Salpingidae, Scolytidae and Trogositidae. Increases in species abundance, especially *Hylastes* spp., *Hylurgops* spp., *Dendroctonus valens, Asemum nitidum,* and *Rhagium inquisitor,* were greatest in the burn only treatment. Relative to controls, total numbers of insects captured were 170, 54, and 45 percent higher in the burn only, harvest and burn and harvest only treatments, respectively. Increases in post-treatment insect species diversity were also apparent in the families Buprestidae (flat-headed wood borers), Cerambycidae (round-headed wood borers) and Scolytidae (bark beetles). The latter families inhabit dead and dying wood and are associated with forest disturbances (Furniss and Carolin 1977). Preliminary results suggest that insect response to restoration treatments is quite species-specific, but that selected species increased dramatically, with responses most pronounced in the burn only treatment, followed by the harvest and burn and harvest only.

Discussion

Overall, species composition of breeding cavity nesters found in this study was similar to that in nearby Idaho Douglas-fir forests (Medin 1985), although nest densities reported here are considerably lower. Lack of replication prevented me from detecting treatment effects; however, preliminary results do suggest that harvesting (either through greater disturbance and/or direct effects on the landscape) was associated with a decline in cavity nest densities and species richness. The white-breasted nuthatch was the only species to breed at a site pre-treatment and then vacate after treatment, while continuing to nest in controls. This response is consistent with Hejl and others (1995) who reported that in the Southwest, this species was less abundant in clearcut and partial cut ponderosa pine stands relative to unharvested forests.

Several species, such as red-breasted nuthatch, mountain chickadee, and red squirrel present in the harvested areas shifted into untreated wildlife tree patches to nest after harvest treatments were completed. Overall, 40 percent of post-treatment cavity nests were located in wildlife tree patches, compared with only 10 percent pre-treatment. These shifts imply that for some species, untreated patch reserves provide preferred habitat relative to partially logged areas. My findings are consistent with studies demonstrating that red-breasted nuthatches and mountain chickadees are more abundant in unharvested forest than in partial cuts (Medin 1985, Szaro and Balda 1979, Waterhouse and Dawson 1998) or in clearcut stands (Hejl 1994, Hejl and others 1995). Both species have been shown to use residual patches. Their detection rates in patches are comparable to those in contiguous forest and greater than in adjacent logged areas (Gyug and Bennett 1995, Seip and Parker 1997). Similarly, red squirrel populations tend to be highest in mature to old unmanaged forests (Carey 1995), and Klenner (1998) demonstrated that partial cutting treatments involving 20-50 percent volume removal are associated with moderate declines, although this species does use patches of residual snags and green trees.

Shifts of cavity nesters into wildlife tree patches suggest that declines in nest density and species richness were partially offset through patch retention. Patches represented only 4.2 percent of the total area harvested in this operational trial. This is 0.3 percent less than area-based retention requirements still in effect (Province of British Columbia 1999). A greater level of patch retention (or a lighter level of treatment) could potentially minimize impacts of harvesting on the resident cavity-nesting guild. Retention should be based on pre-treatment surveys to delineate the most valuable wildlife tree habitat, rather than operational ease.

I did not detect short-term effects of burning treatments on cavity nest densities or species richness, with the exception of some anecdotal shifts in species composition. This lack of effect is consistent with lesser severity of the burn treatment on stand structure and with other studies investigating effects of prescribed fire on breeding birds in pine forests (Bock and Bock 1983, Finch and others 1997, Horton and Mannan 1988). After treatment in 1998, mountain bluebirds moved into the burn only to breed, whereas northern flying squirrels, which bred there in 1997, vacated in 1998. Mountain bluebirds are closely associated with early post-fire conditions (Finch and others 1997, Hutto 1995), and Bock and Bock (1983) found a greater abundance of this species in burns when compared with unburned forests. Conversely, northern flying squirrels are more abundant in mature to old forests (Carey 1995, Klenner 1998, McDonald 1995). Thus, this species may have been displaced in my study owing to reduced habitat suitability or short term disturbance directly associated with prescribed burning. We did not detect the Lewis's woodpecker *(Melanerpes lewis)* in our study area from 1996 to 1998. In 1999, this species was observed incidentally for the first time, which is consistent with its reported association with early post-fire habitats (Hutto 1995, Saab and Rich 1997).

Snag densities differed in pre- and post-treatment settings. Specifically, snag densities were 97, 98, and 50 percent lower in the burn only, harvest and burn and harvest only, respectively. In the two harvested treatments, snags were removed to comply with occupational health and safety regulations (Workers' Compensation Board of British Columbia 1998). At the time of the harvest, the regulations required that all snags in reach of work areas be felled during harvesting operations, unless buffered in wildlife tree patches or surrounded by no-work zones. Snag densities in the burn only treatment were very low prior to treatment (approximately 3.8 sph). However, I observed several smaller (< 30 cm dbh) fallen burnt snags with advanced decay and previously active nests in late April of 1998 after the burn. These fallen snags were most likely destabilized by prescribed fire, and similar declines in snag density have been documented for other prescribed burns: 56 percent decrease by Gaines and others (1958); 35-48 percent decrease by Gordon (1996); and 45 percent decrease by Horton and Mannon (1988). In 1999, it became apparent that prescribed burning killed many smaller (<15 cm dbh) trees in the two burned treatments (82.5 and 87.3 percent reduction in mean layer 4 sph in the burn only and harvest and burn, respectively; Penniket & Associates Ltd. 1998). These smaller trees were intensively used for foraging by woodpeckers in 1999, but were too small to provide suitable cavity nesting habitat (Machmer 2000).

The increased abundance and diversity of insects found in the burn only (and to a lesser extent in the harvest and burn and harvest only) is consistent with other studies that have reported a greater abundance of buprestid and cerambicid beetle larvae in recent fire-killed and/or harvested trees (Amman and Ryan 1991, Evans 1964, Fellin 1980). I anticipate an increase in woodpecker foraging activity on trees in burned areas in future years, as pupae and larvae of the elevated 1998 insect populations become available prey. Monitoring at this site will continue for another 1 to 2 years.

Management Implications

Successful management of the cavity-nesting bird community during broad-scale application of ecosystem restoration treatments will require a multi-faceted approach that satisfies the diverse requirements of various guild members. Recently revised occupational health and safety regulations in British Columbia (Workers' Compensation Board of British Columbia 1998) permit retention of dead trees in all forestry operations, provided they do not pose a hazard to forest workers. To promote populations of cavity nesters that are associated with semi-open stands (e.g., red-breasted nuthatch, mountain chickadee, northern flying squirrel) during restoration treatments, I recommend that managers attempt to achieve a patchy rather than uniform treatment severity during mechanical treatments, and that wildlife tree patches be established in all areas planned for restoration treatment. Consideration should be given to exceeding current area-based retention requirements (Province of British Columbia 1999) in an attempt to approach historical stand conditions and minimize the likelihood of adverse impacts on the cavity-nesting guild. Furthermore, patch-reserves should be delineated based on pre-treatment surveys to identify patches with features of highest demonstrated value to cavity nesters, such as dead trees with broken tops, evidence of internal decay and/or previous cavity use in the largest available diameter classes (Bull and others 1997, Steeger and Dulisse 2002).

To address the needs of species associated with open habitats, such as Lewis's woodpecker and mountain bluebird, an abundance of high value dead trees should be retained as individuals or clumps in the main portion of treatment areas. The latter should represent a range of decay classes favoring the largest diameter stems, which have the greatest longevity during fire and satisfy the requirements of the most species (Finch and others 1997, Raphael and White 1984).

To minimize loss of snags during prescribed fire treatment, constructing fire lines around them (Gordon 1996) and/or using fire retardant to protect these habitat features should be considered.

Preliminary insect responses to the treatments suggest that enhancement of food supplies for cavity nesters associated with burning may be greater for partial cutting in combination with burning than for partial cutting alone. If further monitoring substantiates this difference, then consideration should be given to the establishment of "burn only" patch-reserves within areas planned for "harvest and burn" restoration treatment. After treatment, these patch-reserves would contain a higher density of standing dead trees charred by fire to support dependent insect populations that serve as prey for cavity nesters.

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The Role of Coarse Woody Debris in Southeastern Pine Forests: Preliminary Results from a Large-scale Experiment[1]

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Abstract

We initiated a long-term experiment involving manipulation of coarse woody debris (CWD) at the Savannah River National Environmental Research Park in the upper Coastal Plain of South Carolina. Each of four 9.3-ha plots in each of four blocks was subject to one of the following treatments: removal of all snags and fallen logs, removal of fallen logs only, felling and girdling to simulate a catastrophic pulse of CWD, and control. Removal treatments were applied in 1996, and the felling or snag-creation treatment will be applied in 2000-2001. Monitoring of invertebrate, herptile, avian, and mammalian assemblages and CWD dynamics began immediately after CWD removal and continues through the present. Removal treatments resulted in a fivefold to tenfold reduction in CWD abundance. To date, significant differences among treatments have only been detected for a few animal taxa. However, preliminary results underscore the benefits of large-scale experiments. This experiment allowed unambiguous tests of hypotheses regarding the effect of CWD abundance on fauna. Coupled with studies of habitat use and trophic interactions, the experimental approach may result in stronger inferences regarding the function of CWD than results obtained through natural history observation or uncontrolled correlative studies.

Introduction

Coarse woody debris (CWD) includes standing or fallen dead wood and decomposing root systems. Several studies have generally supported the conclusion that CWD provides an important resource for many animals and plants. However, these studies have often been based on data collected under uncontrolled conditions (Harmon and others 1986). Uncontrolled studies of the effects of CWD on animals

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are susceptible to confounding factors because the same conditions leading to CWD abundance (e.g., wind storms) often lead to increased vegetative growth. Changes in vegetation may positively affect populations of animals through increased cover and food availability. Controlled experiments are, therefore, necessary to produce unambiguous conclusions regarding the effects of woody debris within an ecosystem.

The amount and role of CWD markedly vary among forested ecosystems. The amount and role of CWD in old-growth conifer forests of the Pacific Northwest have been intensively studied, but few studies of CWD in southeastern pine forests exist (McMinn and Crossley 1996a). In general, southeastern pine forests are younger than western conifer forests, with tree species that exhibit smaller maximum sizes and shorter life spans than western species. With shorter rotations, often for pulpwood production, managed southeastern forests have low amounts and small pieces of CWD. Typical volumes of CWD in managed forests of the Southeast are poorly known, but mean volume of CWD in natural pine forests on public land in Georgia is estimated at < 20 m^3 ha^{-1} (McMinn and Hardt 1996). By contrast, some of the highest recorded mean CWD volumes are in old-growth Douglas-fir forests of western Oregon (502 m^3 ha^{-1}; Spies and Cline 1988).

Dead wood also decomposes more quickly in southeastern than northwestern forests because of the humid, warm climate of the Southeast (Barber and Van Lear 1984, Harmon and others 1986). Rapid decay, shorter rotations, and smaller trees combine to produce very different CWD characteristics in the Southeast compared to the Pacific Northwest. Consequently, we expect that the role of CWD as a resource for fauna also differs between the two regions. Because managed southern pine forests typically have low structural and vegetative diversity, coarse woody debris may be particularly important as a refuge and food substrate for animals in this environment.

Woody debris is an ecosystem component amenable to management (McMinn and Crossley 1996a). Indeed, forest management practices lead to changes in the abundance of CWD—planned or not. A workshop entitled “Biodiversity and Coarse Woody Debris in Southern Forests,” held in Athens, Georgia, in 1994 underscored the potential negative consequences of failure to understand the role of CWD in southeastern forests. Understanding the role of CWD in managed loblolly pine *(Pinus taeda)* forests in the Southeast is particularly important because of the predominance of this forest type in the landscape (Schultz 1997). Currently, there are insufficient data to allow specific management recommendations for CWD in managed southeastern pine forests (McMinn and Crossley 1996b).

The purpose of this paper is to present the preliminary results of a manipulative experiment into the role of CWD in southeastern forests. This study is a unique interdisciplinary examination of the importance of dead wood to the biotic community in a largely unstudied environment.

Methods

We initiated an experiment to better understand the importance of CWD to fauna in loblolly-pine plantations of the southeastern Coastal Plain. This experiment has been underway since summer 1996, with annual re-treatment of plots. Re-treatment of plots and monitoring of woody debris and fauna are planned through 2007.

Study Area

This research was conducted at the Savannah River National Environmental Research Park (SRNERP), a 78,000-ha nuclear production facility managed by the United States Department of Energy. The SRNERP is located in Aiken, Barnwell, and Allendale Counties, South Carolina (33°0-25'N, 81°25-50'W). The study area lies in the upper portion of the Coastal Plain Physiographic Province (Fenneman 1938) and is bounded on the west by the Savannah River. Vegetation communities of the SRNERP range along topographic and moisture gradients from freshwater wetlands to xeric sandhills (Workman and McLeod 1990). Pine plantations dominate a majority of the SRNERP; loblolly pine is the most abundant species.

Experimental Design

The study was designed as a randomized complete block with four treatments replicated in four blocks. Blocks were four forest stands chosen subject to the following criteria: forested with approximately 45-year-old loblolly pine plantations; ≥ 76 m from nearest wetland, road, and power line; and able to accommodate four square 9.3-ha plots. Finally, accessibility was considered to allow installation and frequent checking of various traps. Within each stand, we established four square 9.3-ha plots. Each plot consisted of a 6-ha core area used for CWD and faunal surveys, surrounded by a 3.3-ha buffer area subject to the same treatment as the core area. Buffer areas were largely unused for surveys to avoid the influence of edge effects. Timber harvesting was prohibited within 61 m of plots.

Within each stand, each of the four plots was randomly assigned to one of the following treatments: removal of all snags and fallen logs, removal of fallen logs only, felling and girdling to simulate a catastrophic pulse of debris, and control. We defined CWD as dead woody material ≥ 10 cm in diameter and ≥ 60 cm in length. Removals were conducted by a private crew under USDA Forest Service supervision in July/August 1996, February 1997, February/March 1998, and February/March 1999. Annual removals are planned during the winter of each year of the study. The catastrophic treatment, which will result in the addition of fallen logs and snags, is planned for the winter of 2000-2001. We are currently planning the specific management action involved in the catastrophic treatment. Choices include cutting trees to mimic wind breakage, pulling trees down to create tip-up mounds, and girdling trees to create snags. Activities would mimic natural blow-down events or beetle attacks. Preliminary proposals call for the felling of 60-90 m^3 ha^{-1} (340-360 stems ha^{-1}), which is roughly 10 times the current CWD load.

All plots had been thinned between 1991 and 1996. Plots were thinned as necessary in 1996 to achieve a standing basal area of 13.8–20.8 m^2 ha^{-1}. All plots will be thinned at about 10-year intervals throughout the study. Most of the experimental areas had been intentionally burned between 1990 and 1996, although some areas had not been burned since 1972. In the winter of 1999-2000 all plots will be burned to normalize plots with respect to this important factor. Thereafter, plots will be burned at about 5-year intervals.

Two grids of equally spaced markers have been used to orient investigators within the plots. A large-scale 7-by-7 grid, with 50-m spacing, has been used for the monitoring of birds. A small-scale 8-by-8 grid, with 20-m spacing, has aided in studies of small mammals, invertebrates, reptiles, and amphibians. Monitoring of woody debris has also been referenced to the 7-by-7 grid.

Monitoring of Woody Debris

Inventories of fallen logs and snags were completed during the late spring and early summer of 1997-1999 on all plots. All fallen logs and snags were tagged with a unique number. Species or genus, length, sound class (range 1-3 based on wood integrity), and bark presence (percent) were measured for all CWD. When possible, cause of mortality (e.g., lightning) was noted. Number of cavities, diameter at breast height (DBH), and standing integrity (degree to which branches and trunk remain intact) were recorded for snags. Mid-point diameter, degree of ground contact, and shape (round, elliptical, or flat) were recorded for fallen logs. Surveys have been conducted annually to measure recruitment of CWD and note changes in the decomposition of previously marked debris.

Population Responses

Arthropods are being monitored with crawl traps (Hanula and New 1996) and burlap bands on tree boles. Pitfalls are used to capture arthropods on the ground. Crawl traps and burlap bands aid in determining whether CWD is important in maintaining arthropod resources on trees, which are a common foraging habitat for a variety of birds. Fifteen crawl traps per plot are open continuously and samples are collected monthly. Fifteen burlap bands per plot are monitored monthly. Arthropods crawling on the ground are sampled with 15 pitfalls placed throughout each plot and operated for 1 week every other month.

Sampling of amphibians, reptiles, and insectivorous small mammals is being conducted at 3 of the 4 experimental stands, for a total of 12 plots. These animals are monitored using a series of pitfall-drift-fence arrays and snake traps. We are using four Y-shaped arrays (Kirkland and Sheppard 1994) and one X-shaped array (Campbell and Christman 1982) at each plot. Aluminum flashing is used as drift fencing. Interspersed along drift-fence spans are pitfall traps (19-l buckets) and snake traps. All traps are opened and checked daily during a 14-day period in each of winter, summer, and autumn, and a 28-day period in spring. Because frogs and salamanders have been observed to breed within temporary pools within or near certain plots, we have restricted our analyses to adults.

Small rodents and some larger mammals are being sampled with box-style traps at three of the four experimental stands. At each station in the 8 × 8 grid, one Sherman live trap (7.5 × 9.0 × 25.5 cm) is placed on the ground and one Sherman live trap is placed on the nearest (≤ 5 m) tree trunk. Traps on trees are placed in wooden sleeves attached to the tree approximately 1.5 m above the ground. Mosby-type wooden box traps (19 × 19 × 61 cm) are placed on the ground at selected stations. Trapping sessions are conducted every other month and include nine consecutive nights of trapping during the new- to quarter-moon phases.

Birds have been sampled using spot-mapping and nest searches during the breeding season (May to July; Bibby and others 1992) and transect surveys during winter (December to February; Kolb 1965). Both morning and afternoon surveys were conducted during the breeding seasons of 1997 and 1998. Transect surveys were conducted during the winters of 1997-1998 and 1998-1999 (Lohr 1999). In addition to determining population responses, Shannon's measure of diversity (*H'*; Ludwig and Reynolds 1988) also was calculated for bird assemblages at each study plot.

Study of Habitat Use

Use of woody debris by cotton mice *(Peromyscus gossypinus)* was examined in 1997 and 1998 using radio-telemetry and fluorescent-powder tracking (McCay 2000). Locations of mice were noted at night when mice were active, and during the day when mice were inactive. Observations were made in areas where CWD was not manipulated.

Preliminary Results

Sampling and analyses are ongoing. Nevertheless, preliminary results underscore many benefits of large-scale experiments in the study of CWD. Our results also illustrate some problems common in ecological field studies.

Woody Debris Loading

Treatments involving removal of fallen CWD resulted in a greater than tenfold decrease in the density and volume of fallen logs *(table 1).* The treatment involving removal of snags also was successful, reducing snag density by 75 percent and snag volume by 90 percent. There were few differences in the size distribution, decay class, or species composition of CWD among treatments. However, CWD at removal plots was more decayed than at non-removal plots because of the difficulty of removing very decayed logs. Starting with the 1999 removal, very decayed logs located in removal plots will be raked apart if they cannot be removed.

Table 1—*Mean density (No./ha) and estimated volume (m^3/ha) of coarse woody debris at plots in one of four treatments: removal of all woody debris (ALL); removal of fallen logs, but not snags (DOW); catastrophic felling (CAT); and control (CON) in 1998. The catastrophic treatment will be implemented in 2000; thus, neither control nor catastrophic plots had been manipulated in 1998.*[1]

		Down woody debris		Standing woody debris	
Treatment	**N**	**Density**	**Volume**	**Density**	**Volume**
ALL	4	6.3 A	0.35 A	2.1	0.22
DOW	4	8.4 A	0.39 A	8.4	2.18
CAT	4	98.9 B	7.87 B	8.1	2.19
CON	4	94.4 B	6.45 B	8.2	2.04

[1] Means not followed by the same letter were different at $\alpha = 0.05$ (Fisher's least-significant-difference test).

Population Response

We have presently identified arthropods collected in pitfalls for 1 year after initial CWD removal. We captured an average (± SE) of 703 (± 175.6) beetles per plot in control plots and 350 (± 149.4) beetles per plot in removal plots. Flies (control, 165.0 ± 40.1; removal, 91.3 ± 46.8) and spiders (control, 532.5 ± 130.9; removal, 296.0 ± 86.6) showed similar trends. Despite these relatively large differences in higher taxonomic categories, only a few families of arthropods were significantly affected by CWD removal. Pitfall captures of ground beetles (Carabidae; control, 134.0 ± 21.3; removal, 58.5 ± 13.3; $p < 0.03$), silken fungus beetles (Cryptophagidae; control, 192.0 ± 62.1; removal, 30.0 ± 26.5; $p < 0.07$), and bark-gnawing beetles (Trogositidae; control, 19.0 ± 6.2; removal, 1.5 ± 0.5; $p < 0.06$) were lower in the CWD removal than in the non-removal plots.

Studies of amphibians, reptiles, and insectivorous mammals have presently demonstrated no treatment effects *(table 2).* However, mean capture rates of most groups were greater at plots without log removal than plots from which logs were removed. There was relatively strong spatial and temporal variation in these data, which reduced our ability to detect treatment differences (i.e., statistical power, Sokal and Rohlf 1981). Additional sampling should increase our ability to detect an effect of log removal on these forest-floor vertebrates.

Among rodents, only southern flying squirrels *(Glaucomys volans)* varied significantly in abundance among treatments ($F = 6.18$, $df = 3,8$, $P = 0.02$; *table 3).* Relative abundance of flying squirrels was highest in plots from which dead trees had been removed. Because this species commonly nests in tree cavities, we were surprised by this result. Presently, it is unclear whether differences in flying squirrel captures reflect treatment effects, pre-existing plot differences, or differences in sampling ability related to snag removal.

A previous study on the SRNERP demonstrated that increased abundance of CWD was associated with increased abundance of cotton mice and that cotton rat *(Sigmodon hispidus)* populations may also be positively affected by large amounts of CWD (Loeb 1999). Although there were no significant differences in captures of cotton mice or cotton rats *(table 3),* both species appeared to be slightly more abundant in plots where no CWD removal had occurred. Again, spatial and temporal variation may have reduced statistical power to detect differences.

The number of breeding territories of woodpeckers and of all birds combined was lower on plots from which snags were removed than control plots *(table 4).* In particular, removal of snags affected red-headed woodpeckers *(Melanerpes erythrocephalus),* red-bellied woodpeckers *(Melanerpes carolinus),* and Carolina wrens *(Thryothorus ludovicianus).* Breeding bird diversity also was highest on control ($H' = 2.72$) and lowest on all removal ($H' = 2.01$) plots ($P < 0.05$). Abundance of weak excavators and secondary cavity-nesters, as well as birds that nest in vegetation, was not markedly affected by treatments. Likewise, CWD removal apparently had no effect on the bird community during winter (Lohr 1999).

Table 2—*Mean number of captures per 14-day sampling period of taxa of forest-floor vertebrates at 3 replicates receiving 1 of 4 treatments: removal of all woody debris (ALL), removal of fallen logs (DOW), catastrophic felling (CAT), and control (CON).*[1]

	Removal plots		Non-removal plots		
Taxon	**ALL**	**DOW**	**CAT**	**CON**	**F-value**
Shrews	2.93	2.60	3.33	3.87	0.41
Frogs and toads	60.87	53.00	74.87	77.67	0.33
Salamanders	7.13	5.33	8.73	6.93	0.21
All amphibians	68.00	58.37	83.60	84.60	0.32
Lizards	7.53	6.27	5.20	5.93	0.34
Snakes	1.53	1.40	1.00	2.53	1.44
All reptiles	9.07	7.73	6.20	8.53	0.42

[1] *F*-value for tests of the hypothesis in which means did not differ (df = 3,6) is also included. The hypothesis was not rejected for any group at α = 0.05.

Table 3—*Mean number of captures per 1000 trap nights (± 1 SE) of common species of rodents at 3 replicates receiving 1 of 4 treatments: removal of all woody debris (ALL), removal of fallen logs (DOW), catastrophic felling (not implemented to date; CAT), and control (CON).*[1]

Species	ALL	DOW	CAT	CON
Southern flying squirrel *(Glaucomys volans)*	29.10 ± 1.92 A	17.87 ± 0.89 B	21.97 ± 2.88 AB	24.28 ± 1.22 AB
Cotton mouse *(Peromyscus gossypinus)*	15.92 ± 3.50 A	13.49 ± 3.82 A	17.83 ± 4.19 A	16.82 ± 6.16 A
Golden mouse *(Ochrotomys nuttali)*	0.77 ± 0.35 A	1.30 ± 0.89 A	0.61 ± 0.31 A	1.71 ± 1.59 A
Old-field mouse *(Peromyscus polionotus)*	1.17 ± 0.96 A	0.05 ± 0.05 A	0.25 ± 0.18 A	0.54 ± 0.30 A
Fox squirrel *(Sciurus niger)*	1.14 ± 0.44 A	0.93 ± 0.53 A	1.28 ± 0.81 A	0.34 ± 0.81 A
Cotton rat *(Sigmodon hispidus)*	0.03 ± 0.03 A	0.17 ± 0.17 A	0.66 ± 0.39 A	1.14 ± 0.62 A
All	25.33 ± 3.87 A	19.17 ± 4.25 A	24.35 ± 3.74 A	26.41 ± 5.27 A

[1] Means not followed by the same letter were significantly different (α = 0.05; Fisher's Least Significant Difference Test).

Table 4—*Mean number of breeding territories for breeding-bird guilds at plots receiving one of three treatments: removal of all woody debris (ALL), removal of fallen logs (DOW), and control (CON) during 1997 and 1998.*[1]

Breeding-bird Guild	ALL	DOW	CON
Woodpeckers	1.4 A	3.5 A	4.5 B
Secondary cavity-nesters	1.8 A	2.2 A	4.8 A
Understory nesters	5.1 A	5.5 A	7.1 A
Midstory and canopy nesters	9.9 A	11.7 A	12.4 A
All breeding birds	20.1 A	23.5 AB	27.5 B

[1] Means not followed by the same letter were significantly different ($\alpha = 0.05$; Fisher's Least Significant Difference Test).

Study of Habitat Use

Cotton mice selectively used decomposing root systems during the day and fallen logs at night (McCay 2000). One hundred out of 108 unique daytime den sites of cotton mice were associated with some form of CWD, usually decomposing root systems. Because other den sites used by cotton mice elsewhere (e.g., burrows of large vertebrates; Frank and Layne 1992) are not abundant in managed loblolly stands, there were probably few alternatives to decomposing root systems. Analysis of powder trails demonstrated the selective inclusion of fallen logs in the pathways of mice, perhaps because logs are useful in navigation (McCay 2000).

Discussion and Conclusion

Animals responding to CWD manipulation during the first few years of this study were those for which CWD is probably a critical resource (e.g., cavity-nesting birds). Reduction in the volume of CWD in forest stands, especially stands with low ambient amounts of CWD, probably changes the quality of the environment for most animals in subtle ways. Thus, detecting the effects of CWD manipulation in southeastern pine forests may require several years of observation. Because population responses reflect differences present in the first few years after manipulation of CWD, they provide conservative depictions of the long-term importance of CWD in pine ecosystems of the Southeast.

The size of plots used in this study was many times larger than the size of home ranges of most insects, many birds (Gill 1994), and most small mammals (e.g., cotton mouse; Wolfe and Linzey 1977). Thus, this experiment permits inferences concerning demographic responses of these species. In contrast, most studies of the effects of CWD on animals have only permitted inferences regarding microhabitat use (e.g., Planz and Kirkland 1992). Nevertheless, even the large plot size used in this study was too small to test population-level responses of highly mobile species, such as the fox squirrel.

The large size of plots in this study precluded the establishment of more than four replicates within each treatment. Furthermore, the effort that was required to sample animals within these large areas precluded the use of all four replicates for the study of some groups (e.g., small mammals). Low replication, coupled with expected temporal and spatial variability, reduced our ability to detect all but the most drastic changes in animal populations during the first few years of study. Over time, however, we expect our ability to detect treatment effects to increase as differences become larger.

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Girdled versus Bark Beetle-created Ponderosa Pine Snags: Utilization by Cavity-dependent Species and Differences in Decay Rate and Insect Diversity[1]

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Abstract

Snags are a natural component of forest ecosystems and provide a variety of functions and values to forests and their constituents. Snags provide important feeding substrates, nesting sites, and habitat for a variety of invertebrates and vertebrates, and many of these functions continue after the snag eventually falls and becomes a log (coarse woody debris). Some forest landscapes are thought to be "snag deficient" for wildlife needs because of the direct action of forest managers or because of natural events such as winter storms or fire. Therefore, it is not unusual for forest managers to desire to create snags by various means. In this study we compared snags created by mechanical girdling (chainsaw) and bark beetle (western pine beetle aggregation pheromone) attack to determine acceptability and suitability to cavity dependent species, tree decomposition characteristics, and insect diversity. After 6 years we have found differences in the rate of deterioration (tree fading rates, branchlet retention, bole failure, top breakage, bark sloughing), woodpecker feeding activity, cavity excavation, and insect diversity. Our data indicate that bark beetle-killed trees provide a more biologically rich snag that is both suitable and acceptable to cavity dependent species.

Introduction

Snags are a natural component of ecosystems that have a variety of values to sustainable forest ecosystems. Snags provide important feeding substrates, nesting sites, and habitat for a variety of invertebrates and vertebrates, and these functions continue long after the snag eventually falls and becomes course woody debris (Laudenslayer 1997, Thomas and others 1979). Historically, snags have been removed from the forest to meet a variety of objectives, including timber production,

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removal of hazardous trees, and to reduce the potential of crown fires. Currently, snags in many areas appear to be in low numbers for wildlife use, and managers may need to create snags to meet management objectives. Methods for stressing trees to kill them for this purpose have been the subject of several studies (Bull and others 1981, Bull and Partridge 1986, Conner and others 1981, Parks and others 1996). Some of these methods can be expensive and hazardous (topping trees with chainsaws and explosives) (Lewis 1998) or could be environmentally problematic (application of chemical herbicides). Less understood, however, are factors, many of them episodic (i.e., fire and insects), affecting the process of snag creation and longevity (Morrison and Raphael 1993).

Prime among these factors, in addition to the nature of the stress causing death, is the physiological condition of the tree when the stress occurs. Among the factors influencing tree stress are tree condition, tree size (age), and the season at which the stress occurs. Together, these factors probably determine in large part the particular sequence of decay-promoting organisms (i.e., insects and fungi) invading the tree as it is dying and afterward. This invasion sequence likely has a strong influence on how quickly the tree dies, how long the resulting snags stand erect, and those characteristics affecting its suitability and acceptability for use by wildlife. It is thus important to understand the process of snag creation, and the factors affecting it, in both artificially and naturally created snags. In this experiment we examined some of these processes.

To the extent possible, processes used to create snags should mimic natural processes to ensure resulting snags are ecologically optimal. In other words, these snags should contribute to a fully functional forest rather than simply meeting snag standards for wildlife. However, technical factors, such as safety and cost, are also important. Two likely methods for creation of snags are girdling and baiting with bark beetle pheromones. Bark beetle pheromones are chemical messengers between conspecifics that create a mass attack on an individual tree for the purpose of killing it (Bedard and Wood 1974). Commercially available pheromones that are species-specific can be deployed in an economic and safe manner that creates a mass attack on a target tree (Browne 1978, Byers 1989). Resulting tree death can be rapid and is followed by an apparently natural sequence of secondary insects, fungi, other arthropods, and vertebrates. This method thus closely mimics natural tree killing by bark beetles.

Mechanical girdling, while technically acceptable, does not closely mimic natural tree death. Girdled trees may not die promptly or at all. Snags created by girdling may be structurally weakened and fall sooner (Bull and Partridge 1986). In California, neither method has been adequately investigated in the large diameter trees favored by woodpeckers as nesting sites (Landram and others 2002, Laudenslayer 1997).

This study investigates processes of snag formation in trees killed by girdling or with bark beetle pheromones with the goal of developing methods that are both technically and ecologically optimal. Specifically, the objectives were to compare the differences between girdled and bark beetle-killed trees relative to the use by cavity-dependent species, decomposition rate, and diversity of insect fauna. We were also interested in whether season of death or diameter of tree had an influence on these variables.

Methods

This study was conducted at the Blacks Mountain Experimental Forest (BMEF) located within the Eagle Lake District of the Lassen National Forest in northeastern California. It was an adjunct study to an interdisciplinary research program also sited within BMEF. This large, long-term research program compares the effects of treatment combinations that include, vegetation structure, livestock grazing, and prescribed fire on forest ecosystem structure and function. BMEF lies ~60 km northwest of Susanville, California, in the eastside pine type. This forest type is representative of a forest assemblage that extends north from Baja California into central British Columbia and is characterized by temperature extremes, low average annual precipitation, and episodic fire. Growing sites tend to be uniform in slope and exposure. The forests of eastside pine are growing on volcanic soils characteristic of the region. BMEF includes a relatively large acreage of old-growth pine forests that, except for fire exclusion, have not been extensively altered.

Except as noted, experimental trees consisted of 48 ponderosa pine (*Pinus ponderosa* Laws), 24 in each of two diameter classes (38-64 and >76 cm dbh). Eight (4 in each dbh class) trees, each no less than 100 m from other groups, will constitute an experimental plot or block. The six plots were selected on the basis of having a high stand complement of ponderosa pine with adequate representation of the diameter classes defined above. Half of the trees within each dbh class on each plot were assigned at random to one of the following treatments:

- Girdling: Two girdling chainsaw cuts, 20 cm apart, and 5 cm into the sapwood were made 61 cm above ground level. Bark and phloem were removed between the chainsaw cuts to prevent healing.
- Pheromone-baiting: A pheromone dispenser obtained from Phero Tech Inc., containing the western pine beetle (*Dendroctonus brevicomis* Leconte) aggregation pheromone, was fixed to the bole of each tree at 2 m above the ground. The western pine beetle aggregation pheromone dispenser contains specific amounts of exo-brevicomin, frontalin, and myrcene. Baits were placed during times of western pine beetle flight that was determined by baited monitoring traps placed in the general vicinity.

Half of the trees in each of the above treatment combinations on each plot were assigned at random to spring (June 1993) and half to fall (September 1993) treatment periods. Thus, there will be one tree with each snag creation method by dbh by time of treatment combination.

Pheromone treated trees were monitored every 2 to 3 weeks after bait placement to assess the progress of mass attack by western pine beetle. All trees in all treatment combinations were visited every month post-treatment (except during the winter) to assess fading rates (foliage color changed) during the first year and then twice yearly thereafter. Pheromone baited trees were judged to be successfully attacked by western pine beetle when more than 50 red pitch tubes could be counted in the lower 4 m of the bole. Pheromone baits were then removed.

One, two, three and five years after baiting and girdling, each tree was visited to assess the amount of secondary insect and woodpecker activity. Insect activity was monitored by Lindgren funnel traps hung on pulleys next to the bole of the tree at three heights (dbh, 6 m, and 12 m). Insects from these traps were collected approximately every 2 weeks from June to September from 1993 to 1997. They were identified to either order or family, counted, and selected specimens were mounted for future reference. In 1995 each tree was also assessed for emergence of secondary insects. This was done by counting and characterizing the shape and size of emergence holes (Furniss and Carolin 1977) on the surface of the bole that fell within a 30 X 30 cm template. The template was placed at dbh and 4 m above the ground. The circumference of the bole at each height was divided as closely as possible to 12-inch segments, and the site of sampling was randomly selected.

Flaking of bark by woodpeckers is used to extract prey items from within the bark and is defined as pieces of bark being chipped away from the bole. Flaked areas can be readily recognized by the discolored area of the bark. The bark surface remains relatively flat in contrast to feeding holes drilled by a different woodpecker feeding activity. Drilling is defined as woodpecker action that actually drills a hole through the bark to the xylem tissue to access prey. The hole is wider at the surface and narrows as it reaches the xylem. The surface of the drilled hole is ragged and uneven. Chips from both methods accumulate around the base of the tree. During surveys the presence or absence of the two woodpecker feeding activities on the experimental trees was recorded.

Beginning in the fall of 1994 and each year thereafter, all trees were visually inspected for the presence of nesting cavities. Full cavities are defined as an almost perfectly round excavation in the bole of study trees with perceptible depth to the hole. A cavity start is defined as a full cavity where the excavation has little depth but does reach the xylem tissue. Observers used various types of binoculars to make these inspections.

In 1999 in addition to rating the type and degree of woodpecker activity, observers also assessed tree decomposition characteristics. The amount and location of bark sloughing was noted as well as whether there was top breakage. Sloughing of the bark is defined as the bark separated from the xylem and either falling away from the bole or sliding apart. Either action exposed the xylem tissue. Finally, each study tree was observed for the presence or absence of branchlets. These are defined as the outmost woody tissue on each branch. These data were taken in 1999.

We are in the sixth year of this continuous study and much data has been collected. In this paper we only present a portion of the data collected, mostly in the form of qualitative observations.

Results and Discussion

Three years into this study there appeared to be no difference between spring- and fall-treated trees for any variable tested; therefore, the treatments of interest became method of snag creation and diameter class. There was no significant difference in mean tree diameter for each of the two classes between the methods used to create snags *(table 1).* All the ponderosa pine trees baited with western pine beetle aggregation pheromone were successfully attacked by western pine beetle and no additional adjacent trees were attacked. One tree within the pheromone baited/small diameter treatment group failed to be attacked because it was misidentified as a ponderosa pine when in fact it was a Jeffrey pine *(Pinus jeffreryi* Grev. and Balf.). Consequently this tree was not considered as part of the experiment. Bark-beetle killed trees faded rapidly whereas girdled trees showed no sign of needle fade for 23 months. Those trees baited with pheromones in July of 1993 turned yellow or straw colored by August/September of the same year, whereas those trees baited in September began to fade in late-June/early-July 1994.

Secondary insects including adult members of the family Buprestidae (primarily *Melanophila* spp.), Cerambycidae (in particular *Ergates* spp and *Monochamus* spp.), Elateridae, and Bostrichidae were captured in the Lindgren funnel traps from both girdled and pheromone-baited trees. However, the numbers of insects captured from girdled and pheromone-baited trees were considerably different. An example of the difference in numbers of emerging woodboring insects collected from the two treatment groups is presented in *table 2*. By September 1995, over 2 years after treatment, the number of emergence holes counted in the 12 large diameter pheromone-baited trees were approximately 16 to 20 times greater than occurred on those trees that were girdled. This same relationship, albeit with a somewhat smaller difference, also occurred on the small diameter trees for both snag creation methods. Colonization by red turpentine beetle (RTB) *Dendroctonus valens* LeConte on both treatment groups also appeared to be different. Typically RTB attacks occur at the base of trees and usually follow colonization by western pine beetle or other primary *Dendroctonus* attacks. They also are quite common in trees of sufficient diameter that have been injured by fire (Furniss and Carolin 1977). Experimental ponderosa pine baited with pheromone averaged 74.6 attacks by RTB compared to 23.6 attacks on the girdled trees.

Tree decomposition appeared to be quite different for some variables, depending on whether the snag tree was girdled or killed by bark beetles. Of the 24 trees in the girdled treatment, three trees have fallen. Two of the trees belong to the small diameter group and the remaining tree was a large diameter tree. Two of these trees (one in each of the diameter groups) were uprooted and one tree broke at 0.6 m above ground level. In the pheromone-baited treatment four trees have fallen: two within the small diameter group and two in the large diameter treatment. One tree (small diameter) was uprooted and three trees broke at 1.5 (small diameter), 10.6, and 15.5 m (both large diameter) above ground level. We consider the latter trees as viable snags as evidence by the occurrence of cavities in each. Girdled trees showed a lower percentage of bark sloughing and a higher percentage of branchlets still present than pheromone-baited trees 6 years after treatment *(table 3).* Neither observation is surprising considering that the girdled trees did not begin to fade or show outward signs of mortality (i.e., fading) until 23 months after girdling.

Table 1—*Mean (+/-sem) diameter at breast height and range for all ponderosa pine trees in girdled/pheromon- baited/diameter/treatment combinations.*[1]

Treatments	N	Mean (+/-sem)	Range
Girdled			
Small diameter	12	18.90(0.83)a	15.1 – 24.0
Large diameter	12	40.80(2.73)b	30.1 – 62.4
Pheromone			
Small diameter	12	19.14(0.76) a	15.6 – 24.4
Large diameter	12	37.31(1.98)b	30.1 – 51.6

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[1] Means followed by the same letter are not different from each other at alpha=0.05 by one-way ANOVA using Bonferroni mean separation test.

Table 2— *Number of emergence holes made by secondary insects from girdled and bark beetle-killed ponderosa pine trees 2 years after treatment, 1995. The number is the sum of the holes counted in a 30.4 cm X 30.4 cm template, one at breast height (DBH) and the other at approximately 4 m above the ground.*

Girdled large diameter			Baited large diameter		
Tree No.	DHB	4 m	Tree No.	DBH	4m
5	0	0	6	1	12
11	0	0	8	8	14
14	0	0	13	2	11
15	0	0	16	0	8
21	0	0	22	14	21
24	0	0	23	3	7
29	2	6	31	4	3
30	2	6	32	7	8
38	0	0	37	2	12
40	0	0	39	17	13
45	0	0	46	4	3
48	0	0	47	19	1
Mean	.33	1.0		6.75	10.91
+/- sem	0.22	0.67		1.87	1.43

Table 3—*Percent of trees in each treatment group according to tree decomposition characteristics, woodpecker activity, and presence/absence of cavities, 1999, 6 years after treatment.*[1]

Treatment	GSD	GLD	PSD	PLD
Bark sloughing	18	9	66	66
Presence of branchlets	100	100	40	50
Flaking	0	0	100	100
Drilling	58	75	66	100
Cavity starts	0	0	33	33
Cavities	0	0	44	44

[1] GSD – Girdled, small diameter; GLD – Girdled, large diameter;
PSD – Pheromone, small diameter; PLD – Pheromone, large diameter.

Trees killed by colonization by western pine beetle clearly showed considerably more woodpecker activity than girdled trees *(table 3).* Whereas 100 percent of the trees baited with western pine beetle pheromones showed evidence of the flaking feeding behavior, none of the girdled trees had evidence of this behavior *(table 3).* All trees baited with pheromones in the spring of 1993 had woodpecker feeding activity (flaking) by September of that year. For those trees baited in the fall of 1993 all showed woodpecker activity by July of 1994. It seems reasonable to assume that the flaking feeding behavior is aimed at capturing pre-emergent western pine beetle adults. It is characteristic of this bark beetle to turn out into the outer bark in the early larval stage, where it continues development, pupates, and rests as a callow adult prior to emergence (Furniss and Caroline 1977, Miller and Keen 1960, Stark and Dahlsten 1970). Thus, these insect stages would be readily available to foraging woodpeckers flaking or scaling. The precise method by which woodpeckers find these areas of dense prey is unknown. Several of the authors (PJS, WFL, RB) have observed numerous occasions where large areas of the bark of lodgepole pine have been removed down to the xylem tissue by woodpeckers in search of mountain pine beetle (*Dendroctonus ponderosa* Hopk.) larvae, pupae and callow adults.

Drilling is the other feeding behavior recorded to measure woodpecker feeding activity. The percentage of trees showing this type of feeding activity varied across all treatment groups *(table 3).* It should be noted however that 100 percent of the large diameter trees that were baited with pheromones had feeding behavior characterized as drilling. We point out also that the number of holes drilled by woodpeckers varied greatly across treatments. Those trees killed by western pine beetle, regardless of diameter class, showed considerably more drilled holes than the trees that were girdled. Of the 12 trees in the girdled/small diameter treatment group that showed evidence of woodpecker drilling, seven trees had two to seven holes each. In the girdled/large diameter treatment, 10 of the 12 trees showing evidence of woodpecker drilling had one to nine holes each. In contrast none of trees in pheromone baited treatments (small and large diameter classes) had fewer than 15 drilled holes in any tree. Several (8) pheromone baited/large diameter trees had > 350 woodpecker holes, whereas no tree in the girdled treatment group had in excess of 60 holes.

The construction of cavities in snags is the definitive answer to whether snags, artificially created or not, are acceptable and suitable to cavity-dependent species. In this study the data as of 1999 strongly suggests that bark beetle-killed ponderosa pine offer those characteristics that are acceptable and suitable to these vertebrates. Six years after pheromone-baiting, 44 percent of the trees in both diameter classes had full cavities compared to no cavities in the girdled treatment groups *(table 3).* Further, an additional 33 percent of the pheromone-baited snags had cavity starts, while no cavity starts where found in the girdled snags *(table 3).* In those pheromone-baited snags that had cavities, the number of cavities in any particular tree ranged from one to eight. Those trees that had multiple cavities were always found in the large diameter class, and a high proportion (62 percent) of the cavities were found in the upper 50 percent of the bole.

It is apparent that not all snags/trees are suitable for wildlife. The results of this study differ somewhat from others (Bull and Partridge 1986, Bull and others 1981, Chambers and others 1997, Conner and others 1981, Parks and others 1996) that investigated various means of creating viable snags needed by cavity-dependent species. The percent of cavity construction was higher in the bark beetle-killed trees; none of the girdled trees were used by woodpeckers as sites for cavities as was seen in previous studies. However, even in this study many questions remain. For instance, do secondary insects, particularly woodborers, carry inoculum for sapwood and heart rots into the tree that make a particular site favorable for cavity excavation? In the process of using bark beetle-killed trees as feeding sites, do woodpeckers become favorably inclined to use these as cavity trees? Unfortunately, little information exists to answer these questions and many others. Research and monitoring are needed to evaluate wildlife use of created snags both at the individual snag/tree and landscape levels.

When selecting a particular method of creating snags in snag deficient areas, land managers must consider a number of factors. Whether the particular method creates a snag that the targeted wildlife will use is crucial. We point out that snags created by bark beetle colonization serve multiple objectives. First, these snags serve as feeding sites from the time they are colonized by a particular bark beetle species, and then for a number of years after this event as secondary beetles cycle through the snag. Second, they serve as suitable sites for cavity excavation that are used by a number of different cavity-dependent species.

Lewis (1998) points out that safety and economics are other factors that land managers must consider when selecting a method to create wildlife snags. He suggests that blasting and saw-topping are both extremely dangerous, in addition to being costly, compared to basal and crown girdling and fungal inoculation. The use of bark beetle pheromones is quite inexpensive. Western pine beetle pheromones cost approximately $8.00/unit and can be used several times if stored properly, and no machinery is needed as with girdling. The most obvious concern about the use of bark beetle pheromones is whether or not their use could create unwanted bark beetle mortality. Although the probability of starting a bark beetle epidemic (local or otherwise) with their use is remote, common sense should be used. If local populations are sparse and stand and tree conditions are thrifty, there is little risk in using bark beetle pheromones. In this study no collateral mortality was associated with either pheromone baiting or girdling. Conversely, if local populations of bark beetles are rising or locally epidemic because of droughty conditions or other predisposing conditions, this method of creating snags should be used with great care.

Finally, whatever method is used to create wildlife snags to meet standards and guides concerning snag densities, the resulting snags must be suitable and acceptable to the wildlife species of concern.

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The Role of Disturbance in Creating Dead Wood: Insect Defoliation and Tree Mortality in Northeastern Oregon[1]

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Abstract

Knowledge of natural disturbance factors that influence ecosystems over large temporal and spatial scales is essential for understanding interactions among ecosystem processes. Repeated assessment of forest stand structure after disturbance events may aid in identifying ecosystem processes and components affected by disturbance that are not readily apparent until long after the disturbance event. In northeastern Oregon, conifer defoliation by phytophagous insects occurs over large temporal and spatial scales and often leads to tree mortality. The current composition and stand structure in mixed conifer stands were documented after two such disturbances: stands 23 years after defoliation by Douglas-fir tussock moth (*Orgyia pseudotsugata* McD.) in the Wenaha-Tucannon Wilderness, and stands 12 years after defoliation by the western spruce budworm (*Choristoneura occidentalis* Freeman) in the Starkey Experimental Forest. Assessment of these areas includes the density of snags, the density and size of down logs, and the change in associated vegetation. The research suggests that similar patterns of stand dynamics, including tree mortality and eventual conversion of standing dead to down logs, along with new seedling establishment, can result from defoliation events with vastly differing durations. This work provides valuable insights into the role of large insect outbreaks and the dynamics of dead wood in these mixed conifer stands.

Introduction

Knowledge of natural stand-replacement disturbances over large temporal and spatial scales is essential for understanding the interactions among ecosystem processes, such as nutrient cycling, plant competition and community development, and wildlife habitat and population dynamics. In the Blue Mountains of northeastern Oregon and southeastern Washington, natural stand-replacement disturbances in mixed conifer stands of grand fir *(Abies grandis* [Dougl. ex D. Don] Lindl.), Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and western larch *(Larix occidentalis* Nutt.) primarily occur as either wildfire (Agee 1993) or insect herbivory (Hessburg and others 1994, Wickman 1992). The largest Douglas-fir tussock moth *(Orgyia pseudotsugata* McD.) outbreak on record occurred in this area between 1972 and 1974, resulting in about 3,240 km^2 of defoliation (Brookes and Campbell 1978,

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Graham and others 1975, USDA 1978). Grand fir and Douglas-fir that were stripped of foliage for more than 90 percent of their crown length died (Wickman 1978). Patches of dead trees were scattered throughout the outbreak area. Federal and State land managers and private landowners initiated chemical control programs to reduce larval densities and salvage harvesting of timber to reduce fuels and capture tree volume. In the early 1980s, a western spruce budworm *(Choristoneura occidentalis* Freeman) outbreak began in northeastern Oregon. Stands throughout eastern Oregon and eastern Washington eventually were infested, resulting in about 28,300 km^2 of defoliation (USDA Forest Service 1988). Again, salvage harvesting of timber and aerial spray programs occurred throughout the two states.

Studying the long-term effects of natural disturbances such as Douglas-fir tussock moth or western spruce budworm outbreaks requires assessment of stand dynamics over several decades. It also requires assessment of stands that remain relatively undisturbed by human activities or management. After the recent Douglas-fir tussock moth and western spruce budworm outbreaks, managers were increasingly concerned about long-term ecological effects, especially the changes in stand structure and the accumulation of dead and down wood that may increase fire hazard. Many opportunities to evaluate long-term changes, however, were compromised by management activities, including harvesting and aerial spraying. Two areas in northeastern Oregon in which natural processes were not altered by management activities were recognized at the onset of the respective outbreaks and thus provide an opportunity for long-term assessment. A study site at Grizzly Bear Ridge, in the Wenaha-Tucannon Wilderness Area, Umatilla National Forest, was established in 1972 during the early phase of the Douglas-fir tussock moth outbreak. A similar site at Bally Mountain, in the Starkey Experimental Forest, Wallowa-Whitman National Forest, was established in 1983 at the beginning of the western spruce budworm outbreak. Both sites have a multi-century history of insect-caused defoliation (Swetnam and others 1995). The original study objectives at both sites were to assess host tree mortality and damage such as top-kill and growth loss, and stand dynamics and compositional changes including natural regeneration. The stands were examined annually for 10 years after the outbreaks.

Tree mortality after Douglas-fir tussock moth defoliation occurred over a 5-year period from 1973 to 1977 at the Grizzly Bear Ridge site. Tree mortality after western spruce budworm defoliation occurred over an 8-year period from 1984 to 1992 at the Bally Mountain site. Stands at both sites had similar extreme post-outbreak tree mortality, ranging from 40 to 90 percent tree mortality (Wickman and others 1986).[4] Ten years after the onset of the outbreak, natural regeneration was assessed at Grizzly Bear Ridge. About 1,230 new seedlings per hectare were counted, of which 60 percent were grand fir (Wickman and others 1986). Wickman and others (1986) suggested that, in the absence of fire, the stand structure would be conducive to supporting the next Douglas-fir tussock moth outbreak in 70 to 90 years.

With increasing recognition of the importance of snags and logs for wildlife habitat (Bull and others 1997, Maser and others 1979) and ecosystem processes, such as the role of nonsymbiotic nitrogen fixation in nutrient cycling, coarse woody debris in ectomycorrhizae relations, and long-term carbon storage (Harvey and others 1987, Jurgensen and others 1992), we expanded the original study objectives to include assessment of the dead wood component. In 1995, we re-examined stand structure at

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[4] Unpublished data on file at the Pacific Northwest Research Station, LaGrande, Oreg.

the Grizzly Bear Ridge site, focusing on natural regeneration, snag and log distribution, and plant community composition. This represented a 23-year postoutbreak assessment of stand conditions. In 1997, we re-examined stand structure at Bally Mountain, focusing on establishment of natural regeneration and snag and log distribution. This represented a 12-year postoutbreak assessment of stand conditions.

In this paper, we describe stand conditions at both Grizzly Bear Ridge and Bally Mountain, emphasizing the dead wood component. We believe these results have relevancy as individual case studies of typical Blue Mountain mixed-conifer stands subjected to extreme defoliation after which natural processes of mortality and down wood recruitment were allowed to proceed unhindered by management activities.

Study Area and Methods

Stand structure after Douglas-fir tussock moth defoliation was examined on Grizzly Bear Ridge in the Wenaha-Tucannon Wilderness *(fig. 1).* The study site (latitude 45° 59' 45", longitude 117° 44' 30") is on a gentle south-facing slope and broad plateau at about 1,280 m elevation, above steep Wenaha River canyon “breaks.” At the onset of the last Douglas-fir tussock moth outbreak, these stands were composed of mature grand fir and Douglas-fir as well as minor amounts of western larch and ponderosa pine, totaling about 830 trees per hectare and 58 m^2 per hectare of basal area. Ten years after the outbreak, the live residual overstory consisted of about 370 trees per hectare and 23 m^2 per hectare of basal area (Wickman and others 1986). The study area conforms to the grand fir/twinflower plant association as described by Johnson and Clausnitzer (1992).

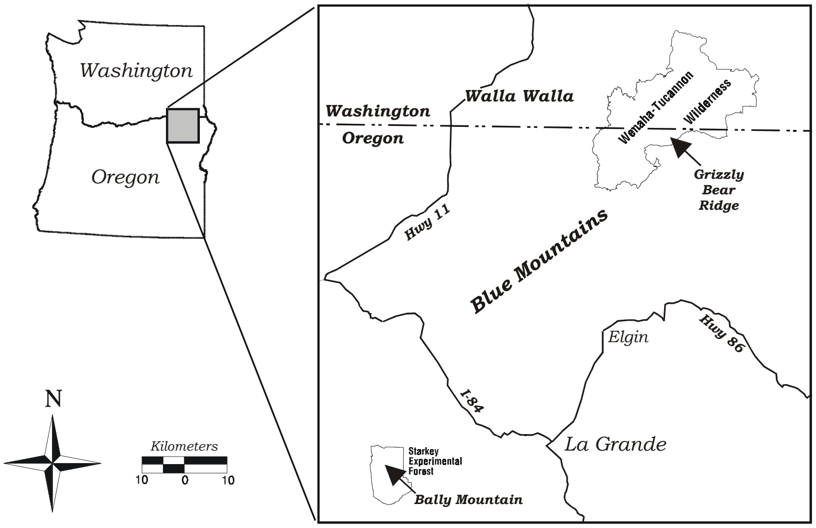

Figure 1—Grizzly Bear Ridge and Bally Mountain study areas for assessing long-term changes in stand structure after severe insect-caused defoliation, northeastern Oregon.

Assessment of stand structure in 1995 was made by using the same sample grid used in 1972 to assess tree mortality and top-kill (Wickman 1978) and later used to document natural regeneration (Wickman and others 1986). Thirty-four circular sample plots, each 81 m^2 (1/50 acre) in size, were systematically located at 30-m intervals along eight transects in two stands. Diameter at breast height (1.37 m high) was measured on all live overstory trees previously tagged, and additional mortality from the assessment in 1986 was noted. All down logs with large-end diameters at least 7.6 cm within the same sample plot were measured for total length to the nearest foot and mid-length diameter to the nearest inch. External and internal wood condition of each log was assessed by using a hatchet to chop into the log at intervals along its length and estimate the percent sound material based on wood hardness, moisture content, and color, and presence of bark (Torgersen and Bull 1995). Heights of all seedlings within a 16-m^2 circular subplot centered on the 81-m^2 circular plot were measured with a height pole to the nearest inch. Total overstory canopy coverage and canopy coverage of all vascular plants by species were ocularly estimated on the same 81-m^2 circular plot.

Stand structure after western spruce budworm defoliation was examined on Bally Mountain in the Starkey Experimental Forest *(fig. 1)*. The study site (latitude 45 ° 17' 30", longitude 118 ° 36' 30") is on a gentle east-facing slope at about 1,417 m elevation. At the onset of the western spruce budworm outbreak in 1983, this stand was composed of 77-year-old grand fir, 165-year-old Douglas-fir and 132-year-old western larch, with minor amounts of ponderosa and lodgepole pine *(Pinus contorta* Doug. ex Loud), totaling about 400 trees per hectare and about 27 m^2 per hectare of basal area.[5] Grand fir represented almost 80 percent of the density and basal area. The study area most closely conforms to the grand fir/twinflower plant association as described by Johnson and Clausnitzer (1992).

Stand structure was assessed at Bally Mountain in 1997 with a sample grid similar to that used at Grizzly Bear Ridge. Seventy-five circular sample plots, each 200 m^2 (1/20 acre) in size, were systematically located at about 30-m intervals throughout a single stand. Diameter at breast height was measured on all live overstory trees previously tagged, and additional mortality from the assessment in 1993 was noted. Because mortality at Bally Mountain was more recent than at Grizzly Bear Ridge, and more of the dead stems remained standing, we did not measure logs directly. Instead, we assumed all broken sections of snags in the plot would fall as logs into the plot, and no sections of snags from outside the plot would fall into the plot. Quantity and size of logs on the ground was estimated by calculating the dimensions of tree boles no longer standing. We measured the height at which snags were broken on all snags with breaks above breast height by using a survey laser. All seedlings within the same plot were counted by species. Because the Bally Mountain site was adjacent to open areas that were grazed by cattle and the understory vegetation was frequently disturbed, we opted not to assess species composition of associated vegetation.

We summarized the data by species at both sites to estimate density, basal area, and diameter class distribution of live and dead stems, and density of logs. For Bally Mountain, we calculated total tree height based on diameter at breast height by using the Lundqvest function with specific parameters for each tree species (Moore and others 1996). We then used the USDA Forest Service's (1999) computer program

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[5] Unpublished data on file at the Pacific Northwest Research Station, LaGrande, Oreg.

NATVOL to estimate the diameter at the top of broken snags and the length and volume of both the standing and down (log) portions. These estimates were based on measured breast-height diameter and snag height and calculated total tree height, using equations for taper and volume within NATVOL by species derived from more than 14,000 trees. For both sites, we calculated the mass of logs, assuming a constant 0.256 kg per m^3 (20 pounds per $foot^3$). Because the amount of cover provided by logs for small vertebrates is related to size of the logs, we calculated the cover as a percentage of total area based on mid-length diameter and total log length at Grizzly Bear Ridge and large end-diameter and total length at Bally Mountain, and assumed no overlap of pieces. Finally, associated vegetation at Grizzly Bear Ridge was summarized by constancy (the percentage of sample plots containing that species) and the mean cover (average of the observed cover values where present).

Results

Live Tree Structure

Residual live trees with overstory canopies occurred on 74 percent of the plots and provided about 44 percent canopy cover at Grizzly Bear Ridge. Total live tree density was about 2,290 trees per hectare and total basal area was about 30 m^2 per hectare *(table 1).* Most of the live stems and basal area was grand fir. More than 65 percent of the live stems at Grizzly Bear Ridge were grand fir seedlings and saplings that contributed little to the total basal area *(table 2).* Average height of natural regeneration (mean and standard error in cm) was 46.6 ± 12.08 for ponderosa pine, 41.6 ± 12.34 for grand fir, 20.9 ± 6.70 for Douglas-fir, 26.2 ± 144.21 for western larch, and 7.2 ± 25.59 for Engelmann spruce.

Live tree density at Bally Mountain was about 560 trees per hectare, of which almost 50 percent was western larch and 30 percent was grand fir *(table 1).* Total basal area was 2 m^2 per hectare. More than 85 percent of the live trees were seedlings and saplings less than 1.37 m tall *(table 2).* Regenerated species included ponderosa pine, grand fir, Douglas-fir, western larch, and lodgepole pine.

Dead Tree Structure

At Grizzly Bear Ridge, there were 109 stems per hectare standing dead, of which 67 percent was grand fir and 20 percent was western larch *(table 1).* Almost 21 m^2 per hectare in basal area of dead trees remained; about 75 percent of this was dead grand fir *(table 1).* Almost 30 percent of the standing dead was grand fir with breast height diameters greater than 50 cm *(table 2).* The largest standing dead grand fir had a diameter of 87 cm. Although infrequently represented, dead ponderosa pine had diameters greater than 80 cm.

Bally Mountain had the same density of standing dead (109 stems per hectare); almost 90 percent of these were grand fir *(table 1).* Total basal area of dead was almost 8 m^2 per hectare and was dominated by grand fir. Grand fir that were dead had diameters that ranged from 6 to 74 cm; about 13 percent were greater than 50 cm *(table 2).* There were 28 dead stems per hectare with tops broken above breast height; more than 80 percent of these were grand fir. Height of the break ranged from 1.5 to 15.8 m (mean ± standard error = 7.1 ± 0.83) for grand fir, 1.7 to 24.4 m (7.0 ± 3.52) for Douglas-fir, and 5.4 to 24.3 m (14.8 ± 9.45) for western larch.

Table 1—*Average density and basal area of standing live and dead trees (mean and standard error) at Grizzly Bear Ridge and Bally Mountain, northeastern Oregon.*

	Number of trees[1]		Basal area[2]	
	Mean	SE	Mean	SE
Grizzly Bear Ridge				
Live stems:				
Pipo[3]	152.6	33.01	--[4]	--
Abgr	1780.6	482.28	24.6	5.383
Psme	243.5	74.04	--	--
Laoc	58.1	18.98	4.75	2.051
Pien	58.1	41.15	0.31	0.311
Total	2292.9	506.82	29.6	5.600
Dead stems:				
Pipo	7.3	5.06	4.07	2.839
Abgr	72.7	20.28	15.4	5.126
Laoc	21.8	15.18	0.97	0.615
Hardwood	3.6	3.63	0.04	0.042
Unknown	3.6	3.63	0.26	0.265
Total	109.0	32.48	20.8	7.430
Bally Mountain				
Live stems:				
Pipo	30.7	5.61	0.22	0.149
Abgr	168.7	40.63	0.60	0.361
Psme	90.7	19.63	0.16	0.159
Laoc	266.7	47.33	1.00	0.354
Pico	6.0	2.50	0.01	0.012
Pien	0.7	0.67	0.00	0.000
Total	563.3	74.67	2.00	0.532
Dead stems:				
Abgr	96.0	9.28	6.82	0.851
Psme	10.7	2.73	0.77	0.335
Laoc	2.7	1.31	0.30	0.202
Total	109.3	10.60	7.89	0.930

[1] Stems ha^{-1}

[2] m^2 ha^{-1}

[3] Species codes: Pipo, *Pinus ponderosa*; Abgr, *Abies grandis*; Psme, *Pseudotsuga menziesii*; Laoc, *Larix occidentalis*; Pico, *Pinus contorta*; Pien, *Picea engelmannii*

[4] – = negligible amount

Table 2—*Cumulative frequency distribution of live and dead stems by diameter class and species at Grizzly Bear Ridge and Bally Mountain, northeastern Oregon.*

	Pipo[1]	Abgr	Psme	Laoc	Pico	Pien	Other
Grizzly Bear Ridge							
Live:							
< bh[2]	6.7	65.6	10.6	0.9	0	2.4	0
0.0 - 9.9[3]	0	1.9	0	0	0	0	0
10.0 - 19.9	0	3.8	0	0	0	0	0
20.0 - 29.9	0	2.4	0	0.3	0	0	0
30.0 - 39.9	0	1.3	0	0.6	0	0.2	0
40.0 - 49.9	0	0.9	0	0.3	0	0	0
≥ 50	0	1.7	0	0.3	0	0	0
Dead:							
< bh	0	0	0	0	0	0	0
0.0 - 9.9	0	3.3	0	3.3	0	0	0
10.0 - 19.9	0	6.7	0	3.3	0	0	3.3
20.0 - 29.9	0	10.0	0	6.7	0	0	0
30.0 - 39.9	0	16.7	0	6.7	0	0	3.3
40.0 - 49.9	0	0	0	0	0	0	0
≥ 50.0	6.7	29.9	0	0	0	0	0
Bally Mountain							
Live:							
< bh	4.7	27.1	13.6	39.3	0.5	0	0
0.0 - 9.9	0.2	2.4	2.4	6.3	0.5	0	0
10.0 - 19.9	0.1	0	0	0.2	0.1	0	0
20.0 - 29.9	0	0	0	0	0	0	0
30.0 - 39.9	0.1	0	0	0.7	0	0	0
40.0 - 49.9	0.1	0.1	0	0.2	0	0	0
≥ 50	0.1	0.2	0.1	0.6	0	0	0
Dead:							
< bh	0	0	0	0	0	0	0
0.0 - 9.9	0	9.8	1.2	0	0	0	0
10.0 - 19.9	0	28.1	2.4	0	0	1.2	0
20.0 - 29.9	0	0	0	0	0	0	0
30.0 - 39.9	0	26.2	3.7	0	0	0	0
40.0 - 49.9	0	10.4	1.2	0	0	0	0
≥ 50.0	0	13.4	1.2	0	0	1.2	0

[1] Species codes: Pipo, *Pinus ponderosa*; Abgr, *Abies grandis*; Psme, *Pseudotsuga menziesii*; Laoc, *Larix occidentalis*; Pico, *Pinus contorta*; Pien, *Picea engelmannii*

[2] Breast height (1.37 m tall)

[3] Diameter class in centimeters

Logs

We measured 210 logs at Grizzly Bear Ridge. Logs ranged in length from 0.6 to 10.1 m (mean ± standard error = 5.0 ± 0.20). Density was 763 logs per hectare, of which 55 percent were identified as grand fir, 14 percent were western larch, almost 2 percent were ponderosa pine, and 28 percent could not be identified to species *(table 3)*. These logs totaled approximately 400 m^3 per hectare in volume, 3,800 m per hectare of linear log length, and 128,800 kg per hectare of mass. Slightly more than 11 percent of the ground was covered by logs. Most of the logs exhibited various indicators of advanced decomposition; 70 percent of all the logs were considered 30 percent sound or less and about 14 percent of the logs were considered at least 80 percent sound. Grand fir logs and those unidentified to species generally were less sound, and western larch and ponderosa pine logs were generally more sound.

Table 3—*Stem characteristics (mean and standard error) of logs by species at Grizzly Bear Ridge and Bally Mountain, northeastern Oregon.*

	Number (Stems ha^{-1})		**Volume (m^3 ha^{-1})**		**Length (m ha^{-1})**		**Mass (kg ha^{-1})**		**Cover (Percent)**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Grizzly Bear Ridge										
Pipo[1]	14.5	8.67	17.4	13.26	64.2	38.97	5582.9	4247.81	0.3	.24
Abgr	425.2	53.50	211.3	49.09	2104.2	325.97	67704.5	15726.72	6.2	1.08
Laoc	105.4	27.67	37.2	14.23	650.9	175.31	11925.1	4558.83	1.4	.40
Unknown	218.0	29.99	136.0	60.61	963.6	153.71	43564.8	19418.96	3.2	.88
Total	763.1	75.13	402.0	76.27	3783.0	404.36	128777.4	22433.49	11.2	1.40
Bally Mountain										
Abgr	51.3	6.64	63.5	27.03	844.1	112.07	20354.6	8659.69	1.3	0.31
Psme	6.7	2.19	2.2	1.09	86.4	30.63	694.9	349.71	0.1	.03
Laoc	1.3	.94	.02	.17	10.8	8.13	67.2	56.04	--[2]	--
Pico	0.7	.67	--	.01	5.3	5.32	--	4.48	--	--
Total	60.0	8.54	65.9	27.02	946.6	128.37	21134.2	8656.87	1.4	.31

[1] Species codes: Abgr, *Abies grandis*; Psme, *Pseudotsuga menziesii*; Laoc, *Larix occidentalis*; Pico, *Pinus contorta*; Pipo, *Pinus ponderosa*

[2] = negligible.

We calculated log characteristics for Bally Mountain based on 48 observed broken snags. Logs were between 4.9 and 50.6 m in length (mean ± standard error = 15.8 ± 0.80). Density was 60 logs per hectare, of which more than 85 percent were grand fir *(table 3)*. Density of Douglas-fir, western larch and lodgepole pine logs was low. Almost all of the log volume (65.9 m^3 per hectare), linear log length (almost 950 m per hectare), and mass (about 21,130 kg per hectare) was from grand fir. Only 1.4 percent of the ground was covered with logs. Large-end diameter of logs at Bally Mountain ranged from 7.1 to 152.4 cm; about 42 percent were less than 15.2 cm (6 inches), 34 percent were between 15.2 and 30.2 cm (6.0 to 11.9 inches), 19 percent were between 30.5 and 50.5 cm (12 and 19.9 inches), and 4 percent were larger than 51 cm (20 inches).

Associated Vegetation

We identified 49 species of shrubs, forbs, and graminoids in the diverse understory at Grizzly Bear Ridge. Common shrubs included *Symphoricarpos albus* (L.) Blake, *Spiraea betulifolia* Pall., *Rosa* species, *Vaccinium membranaceum* Dougl., and *Linnaea borealis* L. *(table 4)*. Common forbs were *Osmorhiza* species, *Galium triflorum* L., *Adenocaulon bicolor* Hook., and the fern *Pteridium aquilinum* (L.) Kuhn. *Calamagrostis rubescens* Buckl. was the most common grass.

Table 4—*Constancy and average cover of important plants at Grizzly Bear Ridge site, northeastern Oregon.*

	Constancy	**Mean cover**
	Percent	
Shrubs:		
Acer glabrum	26	11
Amelanchier alnifolia	29	8
Berberis repens	12	4
Ceanothus velutinus	9	1
Holodiscus discolor	15	5
Linnaea borealis	44	31
Lonicera ciliosa	9	5
Lonicera utahensis	41	14
Ribes lacustre	21	7
Ribes viscosissimum	38	7
Rosa nutkana/R. woodsii	59	21
Rubus idaeus	3	1
Rubus parviflorus	29	13
Salix scouleriana	9	7
Sambucus cerulea	3	1
Spiraea betulifolia	59	11
Symphoricarpos albus	71	32
Vaccinium membranaceum	53	22
Forbs:		
Achillea millefolium	6	15
Adenocaulon bicolor	32	23
Arnica cordifolia	32	5
Chimaphila umbellata	15	1
Clintonia uniflora	12	9
Disporum trachycarpum	3	1
Galium triflorum	47	14
Goodyera oblongifolia	3	1
Hedysarum boreale	9	10

	Constancy	Mean cover
	Percent	
Hieracium albiflorum	3	1
Mitella pentandra	6	28
Osmorhiza chilensis/O. occidentalis	56	8
Pedicularis racemosa	12	1
Pteridium aquilinum	29	48
Smilacina stellata	26	5
Thalictrum occidentale	15	1
Trifolium longipes	18	20
Valeriana sitchensis	29	15
Graminoids:		
Bromus carinatus	9	12
Calamagrostis rubescens	35	10
Carex geyeri	18	3
Carex rossii	12	3
Elymus glaucus	21	4

Discussion

Although currently dominated by grand fir, Grizzly Bear Ridge and Bally Mountain represent relatively dry, mid-elevation sites throughout the Blue Mountains of northeastern Oregon and southeastern Washington on which mixtures of conifers develop as a result of past disturbances. Under historical fire regimes, these sites were dominated by seral species such as ponderosa pine, western larch, and occasionally Douglas-fir that arose from infrequent stand-replacement fires and were maintained by frequent, low intensity, underburning (Agee 1993, Agee 1994, Hessburg and others 1994). Grand fir rarely dominated in these stands; thin bark and low-growing canopies were easily consumed by frequent wildfires that maintained these sites in open, park-like stands. The presence of wildfire was not uniform across the landscape, however, leading to a wide range in fire return intervals. As ponderosa pine and Douglas-fir matured and perhaps became stressed by climatic conditions, other disturbances such as root diseases, mechanical injuries such as lightning strikes, or insects may have caused mortality (Hessburg and others 1994). Douglas-fir tussock moth and western spruce budworm defoliation occurred in these mixed conifer stands periodically, especially as cohorts of grand fir and Douglas-fir reached into the mid- and upper canopy. Landscape-scale outbreaks probably occurred when less frequent wildfire allowed development of relatively uniform mid-canopy strata composed of grand fir and Douglas-fir. Dendrochronology records indicated outbreak episodes of similar periodicity dating back to the 1700s (Wickman and others 1993). Outbreaks likely were smaller in extent than the most recent outbreaks because the food base (primarily grand fir and Douglas-fir) was discontinuous (Hessburg and others 1994).

With the advent of fire suppression efforts shortly after the turn of the century, sites throughout the Blue Mountains like Grizzly Bear Ridge and Bally Mountain have undergone dramatic shifts in structure and composition. Fire exclusion allowed more shade-tolerant species such as grand fir and Douglas-fir to become established and to develop into dominant positions in the stand canopies. In addition, seral ponderosa pine and western larch were harvested to meet a growing demand for clear lumber for home construction, railroad ties, and shipping boxes for agricultural products (Oliver and others 1994, Wickman 1992). Scattered cut stumps at Bally

Mountain suggest past harvesting of individual stems four to five decades ago. Increased densities of grand fir and Douglas-fir provided a more uniformly distributed food base for insects and led to severe outbreaks of Douglas-fir tussock moth and western spruce budworm. At the onset of the Douglas-fir tussock moth outbreak, stands at Grizzly Bear Ridge probably were composed of multiple cohorts of grand fir and Douglas-fir in the overstory and understory, with remnant ponderosa pine and western larch extending above the upper continuous canopy. Our estimate of pre-outbreak density and basal area (about 830 trees and about 58 m^2 per hectare) suggests that these stands exceeded accepted guidelines of stocking levels for managed stands (Cochran and others 1994). Stocking levels at Bally Mountain were lower, presumably because some harvesting had occurred in prior decades, and only a single cohort of grand fir existed.

Our work at Grizzly Bear Ridge and Bally Mountain suggests that similar patterns of stand dynamics can result from defoliation events that have vastly different durations (2 or 3 years for Douglas-fir tussock moth and 8 to 10 years for western spruce budworm). In these two areas, severe Douglas-fir tussock moth and western spruce budworm defoliation of 40 to 90 percent of the crown weakened trees presumably stressed by competition for growing space and moisture. Fir engraver beetle (*Scolytus ventralis* LeConte) and Douglas-fir beetle (*Dendroctonus pseudotsuga*e Hopkins) and perhaps root diseases then followed at Grizzly Bear Ridge, eventually resulting in up to 75 percent mortality in grand fir and Douglas-fir (Wright and others 1984). We noted little additional mortality in our recent reassessment. In both areas, grand fir mortality exists as both standing dead snags and down logs. Our reassessment of structure at Grizzly Bear Ridge indicated over 70 stems per hectare were dead grand fir that remain standing 23 years after the onset of defoliation and mortality. We have no means of quantifying actual fall rates, but our observations of log wood condition suggest that the dead grand fir that remain standing likely are soft snags that will fall within a decade. Species composition of natural regeneration mirrors the live overstory composition at both locations; ponderosa pine, Douglas-fir, western larch, and Engelmann spruce remain in the overstory and occur as seedlings at Grizzly Bear Ridge, and ponderosa pine, Douglas-fir, western larch, and lodgepole pine remain in the overstory and occur as seedlings at Bally Mountain. We made no attempt to differentiate seedling cohorts by age at Grizzly Bear Ridge, although grand fir seedlings established before the outbreak and grand fir seedlings established immediately after the outbreak existed in about equal numbers 10 years after the outbreak (Wickman and others 1986). Our seedling height measurements indicated relatively rapid growth for the shade-intolerant ponderosa pine, and relatively slow growth for shade-tolerant Douglas-fir, and Engelmann spruce. Mean grand fir seedling height (about 47 cm) probably represents a mixture of two cohorts. Grand fir regeneration was abundant at both Grizzly Bear Ridge and Bally Mountain, setting the stage for the next defoliation event.

Although our description of logs is within normal ranges for similar sites in the Blue Mountains,[6] we urge caution in extrapolation. Our census at Grizzly Bear Ridge was based on relatively small plots and involved counting all logs with large-end diameters at least 7.6 cm. Stand composition at the time of the Douglas-fir tussock moth outbreak suggests that these stands were advanced in age with multiple cohorts of grand fir. Scattered hardwoods presumed to be aspen (*Populus tremuloides*

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[6] Unpublished data on file at the Pacific Northwest Research Station, LaGrande, Oreg.

[Michx.]), ponderosa pine, and western larch previously in the overstory had died. Thus, aspen, ponderosa pine, western larch, and grand fir logs already lay on the forest floor before the outbreak. Our census of logs at Grizzly Bear Ridge represents total accumulation of logs since the last stand-replacement fire. In contrast, our census at Bally Mountain was an indirect estimate of log density, based on estimated volume absent in standing snags. This method accounts only for the volume added to the forest floor since the western spruce budworm outbreak and thus underestimates total log resources. Differences in these two methods also account for differences in average log length. Perhaps the most significant aspect of the log survey was the large number of logs at Grizzly Bear Ridge that exhibited indicators of advanced decomposition. Measured logs were all aboveground, intact, and belonged to log structural class 1 and 2 (Bull and others 1997), yet a majority of the logs were characterized as 30 percent sound or less. This probably represents a high incidence of stem decay after defoliation-caused mortality. Relatively uniform height of broken grand fir snags at Bally Mountain also was a result of stem decay in combination with local storm patterns. Difference between species was expected because of different bole and dead crown architecture. Our sample size, however, prevented a rigorous test of this hypothesis.

Our work suggests that dead wood recruitment after a defoliator outbreak follows a pattern of relatively slow recruitment of snags and logs over a long period of time. This slow recruitment of dead wood probably provides a longer-term and more stable environment for many species of wildlife dependent on dying and dead wood compared to more rapid turnover of snags and logs after stand-replacement wildfire.

We described existing associated vegetation at Grizzly Bear Ridge to help characterize the site and to help identify successional pathways after disturbance. In general, plots at Grizzly Bear Ridge contained numerous species we believe are indicative of past disturbance, especially shade intolerant species such as *Holodiscus discolor* (Pursh) Maxim., *Lonicera utahensis* S. Wats., *Symphoricarpos albus*, *Adenocaulon bicolor*, *Hedysarum boreale* Nutt., *Valeriana sitchensis* Bong., *Bromus carinatus* Hook. and Arn., and *Elymus glaucus* Buckl. Surprisingly, the fern *Pteridium aquilinum* became well established and persistent. Collectively, this species composition describes a lush, early-successional community that might develop after complete overstory removal with little ground disturbance. Few of these plant species would persist after a wildfire. Diversity of shrubs and forbs was greater than would be expected after a stand-replacement fire (Johnson 1998) or in mature stands (Johnson and Clausnitzer 1992).

Our case studies at Grizzly Bear Ridge and Bally Mountain have provided unique opportunities to follow stand dynamics after severe insect defoliation and point to the effect of insect defoliation on long-term maintenance of dead wood resources. Despite annual visits during the first decade and frequent visits through 23 years at Grizzly Bear Ridge, our picture of stand dynamics in mixed conifer ecosystems in the Blue Mountains remains incomplete. A large number of stems remain standing at both sites; these stems will continue to fall as stem decay, wind, and cavity-forming wildlife species function to weaken the boles. Further work is needed to quantify fall rates by species and to quantify log dynamics after similar insect outbreaks. Seedlings will continue to grow, eventually developing a full canopy of susceptible host type. And in the absence of wildfire, both Grizzly Bear

Ridge and Bally Mountain will likely support a major insect outbreak, leading to defoliation and stand mortality.

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Importance to Vertebrates

The Value of Coarse Woody Debris to Vertebrates in the Pacific Northwest[1]

Evelyn L. Bull[2]

Abstract

Many species of birds, mammals, amphibians, and reptiles use coarse woody debris (i.e., standing and downed dead wood) for nesting, roosting, foraging, and shelter. Woodpeckers depend on decayed wood to excavate nest and roost cavities in standing trees. Secondary cavity nesters then claim the abandoned cavities for their nesting or roosting. Many of the woodpeckers and secondary cavity nesters use dead wood to forage on forest insects, including bark beetles and defoliators. Characteristics that affect the type and extent of vertebrate use of dead wood include the physical orientation, size, decay state, tree species, and overall abundance. Some species of heartwood decaying fungi create hollow chambers in living trees, which eventually die to become hollow, standing dead trees. Standing trees with hollow chambers are used by Vaux's swifts *(Chaetura vauxi)* for nesting and roosting, pileated woodpeckers *(Dryocopus pileatus)* for roosting, black bears *(Ursus americanus)* for overwintering, American martens *(Martes americana)* for denning and resting, and many other species of small mammals for shelter. Once the trees fall, many of the same species continue to use the hollow structures, except the avian species. Solid logs provide cover or travel lanes for small mammals. Accumulations of logs stacked on top of each other provide important habitat in the open spaces formed under the snow where martens and small mammals spend much of the winter. Large-diameter logs are used extensively by pileated woodpeckers and black bears for foraging on carpenter ants. Extensively decayed logs provide habitat for amphibians and reptiles.

Introduction

Coarse woody debris, which is defined as standing dead trees and downed trees (i.e., logs) and large branches, is a critical element of healthy, productive, and biologically diverse forests. Coarse woody debris provides habitat for many vertebrate species, including birds, mammals, amphibians, and reptiles. Thomas (1979) identified 179 vertebrate species that use coarse woody debris in the Blue Mountains of Oregon and Washington, which represents 57 percent of the vertebrate species breeding there. For those species using standing dead trees, birds dominate the list by number of species, although many mammals and some reptiles and amphibians use cavities as well as other structural features of dead trees. In the Blue Mountains, 39 bird and 23 mammal species use standing dead trees for nesting and shelter (Thomas 1979). Bunnell and others (1997) found that about 25 percent of the vertebrate species in British Columbia used cavities. Harmon and others (1986) state

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that cavity-nesting birds account for 9-39 percent and 8-62 percent of the total bird species in deciduous and coniferous forests, respectively.

Coarse woody debris is formed in a variety of ways. Trees can be killed by fire, insects, decay fungi, flooding, drought, and windthrow. The means by which a tree is killed influences the manner in which it decays, how long the tree will stand, and the rate of deterioration. A strong relationship exists between the kind of decay in a tree and what species can use it, particularly for nesting and foraging. The degree of decay can be translated into structural classes of standing dead trees and downed trees (Bull and others 1997), which may be useful in categorizing the dead wood resources.

In addition to decay, characteristics that affect the type and extent of vertebrate use of coarse woody debris include physical orientation (vertical or horizontal), size (diameter and length), species of wood, and overall abundance of material (Harmon and others 1986). The majority of species that use snags are birds and bats, while the majority of species using downed trees include small mammals, amphibians, and reptiles. The importance of different characteristics of coarse woody debris will be discussed for the following groups of vertebrates: birds, mammals, amphibians, and reptiles.

Birds

Woodpeckers, termed primary cavity excavators, excavate the cavities they use for nesting and roosting. Species using vacated existing cavities are termed secondary cavity nesters. Woodpeckers usually excavate their nest cavities in decayed wood in dead trees because most woodpeckers lack the adaptations (bill structure, cushion in brain, muscle structure) needed to excavate in sound wood. The pileated woodpecker *(Dryocopus pileatus)* is the strongest excavator and can excavate cavities in sound wood, while weaker excavators like the Lewis's woodpecker *(Melanerpes lewis)* require advanced decay before they can excavate a cavity. A woodpecker's preference for a particular tree species for nesting is largely influenced by the specific decay characteristics that occur in that tree species. Live trees can function as dead trees if portions of the wood (e.g., dead tops or large dead branches) contain decay as a result of wounding, lightning, or other injuries. Loose bark on dead trees may also provide nesting crevices for brown creepers *(Certhia americana)* and some secondary nesting birds.

Hollow trees are a unique structural feature in forests. The heartwood in these trees is decayed by heart-rot fungi while the tree is alive (Bull and others 1997). Ninety-five percent of pileated woodpecker roost sites in northeastern Oregon were in hollow trees, and 5 percent were in vacated nest cavities (Bull and others 1992). Pileated woodpeckers excavate entrance holes in these trees to access the hollow chamber. Once an entrance to the hollow chamber has been made, other species like the northern flicker *(Colaptes auratus)* also use these trees for roosting. The great depth of some of these hollow chambers makes them unsuitable for nesting by most birds, except the Vaux's swift *(Chaetura vauxi),* which is dependent on these hollow trees for nesting in forest communities. All 21 swift nest trees located in northeastern Oregon were in hollow grand fir *(Abies grandis).* Swift nest trees averaged 67.5 cm d.b.h. and 25 m tall with an internal hollow chamber that averaged 28 cm in diameter and 5.7 m deep (Bull and Collins 1993).

In a recent study, I placed swift nest boxes (3 m deep and 30-cm square) in trees to simulate hollow trees in three categories of stands: stands of old forest multi-strata (multi-cohort, multi-strata stands with large old trees) in grand fir forest types, regeneration cuts in grand fir types, and mature stands of ponderosa pine. Thirty percent of the bird boxes in old forest multi-strata stands were used by swifts for nesting. Other use included roosting by pileated woodpeckers and northern flickers and nesting by flying squirrels *(Glaucomys sabrinus)* and red squirrels *(Tamiasciurus hudsonicus).*

Size of dead tree can be critical for nesting for some species. Woodpeckers must select a dead tree that is large enough to accommodate the cavity they excavate at a height at which they prefer to nest. Typically, the larger diameter dead trees can accommodate a greater variety of species and stand longer than smaller diameter snags. The larger woodpecker species are particularly important because they create larger cavities that can be used by larger secondary cavity nesters, like the northern saw-whet owl *(Aegolius acadicus).*

Many woodpecker species forage extensively on invertebrates found in dying and dead trees and logs. Woodpecker foraging may effectively reduce populations of some bark beetles (Steeger and others 1998). In northeastern Oregon, 38 percent of pileated woodpecker foraging was on dead trees, and 38 percent was on logs; carpenter (*Camponotus* spp.) and red forest (*Formica* spp.) ants were the primary prey based on analysis of woodpecker scats. Logs preferred for foraging by the pileated woodpeckers were decayed Douglas-fir *(Pseudotsuga menseizii)* or western larch *(Larix occidentalis)* larger than 38 cm in diameter (Bull and Holthausen 1993). Foraging on logs occurs primarily in snow-free months when logs are accessible. Northern flickers forage on logs with a high incidence of decay. Black-backed *(Picoides arcticus)* and three-toed woodpeckers *(Picoides tridactylus)* also forage on bark beetles (Scolytidae) and secondary insects (Cerambycidae and Buprestidae) in logs. Foraging by vertebrates on logs probably peaks toward the middle or late stages of decay when logs are softer and invertebrates and fungal fruiting bodies are more common (Harmon and others 1986).

Although isolated dead trees and logs are used for nesting and foraging, concentrations of dead trees and logs provide better cover and more opportunities for use. Some woodpeckers, like the pileated woodpecker, frequently nest in the same vicinity but use different trees each year. Woodpecker nests in isolated dead trees may be more vulnerable to predators than nests in a cluster of dead trees where predators would have to search more dead trees and other vacated cavities.

Some cavity users may be associated with natural disturbances like fire. Hutto (1995) reported that black-backed woodpeckers seemed to be largely restricted to standing dead trees created by stand-replacement fires in Montana. In southwestern Idaho, Saab and Dudley (1998) found high densities of black-backed and Lewis's woodpeckers in stand-replacement fires in ponderosa pine *(Pinus ponderosa),* although nesting black-backed woodpeckers in northeastern Oregon were not restricted to stands with fire (Bull and others 1986).

Some of the cavity-nesting birds like the pileated and white-headed woodpeckers *(Picoides albolarvatus),* Vaux's swifts, and flammulated owls *(Otus flammeolus)* are associated with stands with large-diameter trees because of their reliance on large trees and other structural attributes of these forests.

Mammals

Dead wood, both standing and down, is important to mammals for cover, denning, and resting. The cavities created by woodpeckers are readily used by red squirrels, flying squirrels, bushy-tailed woodrats *(Neotoma cinerea),* and some bats. Larger cavities in decayed heartwood are used by American martens (*Martes americana),* fishers *(Martes pennanti),* bobcats *(Lynx rufus),* and black bears for denning and shelter. The function of logs depends largely on the extent of decay, their size, and abundance. Logs lacking decay are typically used for cover and runways. As logs decay and the bark loosens, small mammals can burrow into the wood under the bark.

Research in the last two decades has identified the value of cavities in snags for roosting bats. Maternity colonies of silver-haired bats *(Lasionycteris noctivagans)* normally are located in cavities in trees during the summer, although males and nonreproductive females may roost alone in cracks in trees and under bark (Mattson and others 1996, Betts 1998). In northeastern Oregon, trees with cavities that were used by roosting bats were taller, less decayed, and farther from adjacent trees than a sample of available trees; this selection presumably took advantage of the absorption of solar radiation and retention of heat in the trees (Betts 1998). Silver-haired bats are dependent on trees, typically roosting in narrow crevices in tree trunks or under the bark in large trees in Canada (Barclay and others 1988, Nagorsen and Brigham 1993). In southern interior British Columbia, big brown bats *(Eptesicus fuscus)* roosted in hollow cavities in large-diameter ponderosa pine snags (Brigham 1991). Vonhof and Barclay (1996) found that four species of tree-roosting bats (*E. fuscus, L. noctivagans, Myotis evotis*, and *M. volans*) preferred roosts in tall trees associated with lower canopy closure. Of 21 roosts, 14 were beneath loose bark, 5 were in cavities excavated by woodpeckers, and 2 were in natural cavities.

Long-legged bats *(Myotis volans)* in the central Oregon Cascades roosted in large Douglas-fir snags averaging 97 cm dbh and 38 m high (Ormsbee and McComb 1998). Bats in California roosted in basal hollows in old-growth redwood stands *(Sequoia sempervirens)* in both contiguous forests and in small isolated remnant patches (Zielinski and Gellman 1999).

Hollow standing trees, both live and dead, and hollow logs are used extensively by black bears, American martens, fishers, bushy-tailed woodrats, and flying and red squirrels. Hollow trees with either a top-entry or base-entry comprised 22 percent of 165 black bear dens in northeastern Oregon; 12 percent of the dens were in hollow logs (Bull and others 2000). Top-entry den trees averaged 114 cm dbh, while base-entry trees averaged 108 cm dbh. The majority of hollow trees and logs were grand fir, with Indian paint fungus *(Echinodontium tinctorium)* being the primary agent responsible for creating the hollow chambers in these trees.

Hollow trees and logs are particularly important habitat for American martens in northeastern Oregon where 23 percent of 1,184 rest sites of martens were in trees with cavities (mostly hollow trees) (Bull and Heater 2000). Seventy-three percent of natal dens were in hollow trees, while 58 percent and 21 percent of maternal (post-natal) dens were in hollow logs and hollow trees, respectively. These hollow structures provided dry, warm, and secure sites that were inaccessible to most predators.

Many carnivores are associated with dead wood. Logs provide cover for mountain lions *(Felix concolor)* at diurnal bed sites and at natal and maternal den sites (J. Akenson, pers. comm.). Wolverines *(Gulo gulo)* may require coarse woody debris in some habitats for denning (MacKinnon 1998). Lynx *(Lynx lynx)* require mature forests for denning and a high density of logs (Koehler 1990). Logs and stumps may be the most important component of lynx denning habitat because they provide cover for kittens (Koehler and Brittell 1990). Accumulations of logs under snow are used extensively by American martens for hunting and for shelter (Buskirk and Powell 1994). These accumulations of logs are also used by red squirrels for their middens during the winter.

Abundance of small mammals is associated with log cover. On the Olympic Peninsula, abundance of deer mice *(Peromyscus maniculatus),* red-backed voles (*Clethrionomys* spp.), Trowbridge's shrews *(Sorex trowbridgii),* and shrew-moles *(Neurotrichus gibbsii)* increased with coarse woody debris in coniferous stands (Carey and Johnson 1995). Red squirrels are abundant in older aspen stands (Roy and others 1995) and use snags and large trees for nesting and cover and use fungi and lichens growing on coarse woody debris as food.

Red-backed voles use logs extensively for cover and food, eating mostly fungi and truffles, many of which are associated with logs (Ure and Maser 1982). The mean number of captures of this species was positively correlated with mean log diameter and size of log overhang (Hayes and Cross 1987). The larger logs probably provide more protective cover from predators than the smaller ones for traveling voles. In southwestern Oregon, locations of radio-tagged red-backed voles coincided with downed logs 98 percent of the time, even though only 7 percent of the study area was covered with logs. In addition, red-backed voles used logs in the later stages of decay significantly more often than logs in the earlier stages of decay (Tallman and Mills 1994).

Amphibians and Reptiles

At least 16 species of salamanders are associated with forests in Oregon (Bunnell and others 1997). More specifically, three species of predatory salamanders (*Batrachoseps wrighti, Ensatina eschscholtzi,* and *Aneides ferreus*) deposit eggs within logs in coniferous forests in western Oregon, as well as foraging on most invertebrate species found in those logs (Maser and Trappe 1984, Harmon and others 1986). Clouded salamanders *(Aneides ferreus)* are found in large coarse woody debris with loose bark, and their populations are positively correlated with stand age (Aubry and Hall 1991). Ensatinas *(Ensatina eschscholtzii)* are associated with decayed coarse woody debris (Bury and others 1991). Species diversity and abundance among the herpetofauna differed among different forest structures in the Oregon and Washington Cascades (Bury and Corn 1988) and in southwestern Oregon and northwestern California (Welsh and Lind 1988).

Conclusions

Although a great deal has been learned about the importance of dead wood to wildlife and ecosystems in the last two decades, there are still information gaps. The influence of fire, insects, and disease on creating and removing (fire) dead wood across landscapes needs intensive research to understand the dynamics of this ecological component in western forests. Additional information is needed on the density and types of dead trees and their relationships to the density and types of live trees also present that will provide habitat (particularly for foraging) for viable populations of primary and secondary cavity nesters. The best methods for creating dead trees is still an important issue in restoration efforts. Artificially creating hollow trees is as yet not possible, although experiments using inoculation of decay fungi are ongoing.

Limited information on the density and kind of logs is available for many areas, and few studies have addressed the density required to provide habitat for viable populations of small mammals and herpetofauna. Many management plans do not adequately address density of logs, particularly on a landscape level. There continue to be conflicts in management agencies between retaining logs and lowering fuel levels to reduce the risk and extent of wildfire. If maintaining viable populations of species that require high densities of logs (like pileated woodpeckers and American martens) is an important management goal, an integration of managing the risk of wildlfire, the habitat requirements of these species, and the ecological processes resulting from fire is needed.

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Are There Snags in the System? Comparing Cavity Use among Nesting Birds in "Snag-rich" and "Snag-poor" Eastside Pine Forests[1]

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Abstract

We compared the density of snags, snags with cavities, and cavity-nesting bird use at two sites in northern California: Blacks Mountain Experimental Forest, a site with large trees and large snags because of protection from logging, contrasted with the Goosenest Adaptive Management Area, where a century of logging left this forest with few large trees and snags. Indeed, there was a threefold difference between sites in total snags, and a fifteenfold difference in cavity-nesting bird use. However, we feel finding a "snags per acre" prescription is inadequate, as tree size, rate of snag generation, and mode of tree death have been disrupted this past century. We argue that understanding the interactions between fire, bark beetles, woodpecker foraging and excavating, sapwood decay organisms, snag "demography," and cavity-nesting species ecological requirements apart from simply cavities are required in place of simply counting snags in landscapes.

Introduction

The habitat structure and ecological processes for our western coniferous forests have changed dramatically in the past century primarily because of extensive logging and fire suppression. The forests of today often are denser, have a larger component of shade tolerant species, and have fewer large, older trees (Bonnicksen 2000, Covington and Moore 1994). This is particularly true of eastside pine forests of California and Oregon, dominated by ponderosa pine *(Pinus ponderosa)* and Jeffrey pine *(P. jeffreyi)* (Covington and Moore 1994, Laudenslayer and Darr 1990).

The density of large snag trees and the processes of their creation have been greatly altered as well. Logging and salvage logging have reduced densities of potential and actual snags from many landscapes. The suppression of fire has suppressed the naturally prevalent mode of snag generation (Horton and Mannan

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1988). Understanding these changes in the world of snags in forests is important because snags with cavities are essential to wildlife populations. Snags with cavities are needed as nesting sites for many species of birds and are used by other wildlife (Bull 1983, Cline and others 1980, Ganey 1999, Mannan and others 1980, Miller and Miller 1980, Moorman and others 1999, Raphael and White 1984, Scott 1978). The issue of snag management, and prescribing adequate "snags per acre" for wildlife in forests, has been and continues to be a major focus of forest management (Brawn and Balda 1988, Brawn and others 1987, Bull and others 1997, Ganey 1999, Horton and Mannan 1988, Martin and Eadie 1999, McClellan and Frissell 1975, McComb and others 1986, Morrison and others 1986, Ohmann and others 1994, Raphael and White 1984, Ross and Niwa 1997, Scott 1979, Schreiber and deCalesta 1992, Thomas and others 1979, Zarnowitz and Manuwal 1985).

We have been studying wildlife-forest relationships at two sites in northern California (Zack and others 1999). The eastside pine forests at the Goosenest Adaptive Management Area in the Klamath National Forest are more or less "typical" in that they have been logged and fire suppressed this past century, resulting in a dense forest with few large tree and few snags. In contrast, the eastside pine forests of the Blacks Mountain Experimental Forest in the Lassen National Forest, particularly those in the Research Natural Areas, have not been extensively logged (but have been fire suppressed), and so contain many large pine trees and snags (Oliver and Powers 1998).

In this paper, we compare the abundance of snags and snag cavity use at these sites from data collected in 1999, and discuss the implications of our results for eastside pine forest management and wildlife. We also present data on bark beetle and woodpecker foraging patterns in relation to snags and cavity prevalence.

Methods

This study was conducted at two sites in northern California: the Blacks Mountain Experimental Forest (BMEF), in the Lassen National Forest, northeast of Lassen National Park, and at the Goosenest Adaptive Management Area (GAMA), Klamath National Forest, east of Mount Shasta. These sites are currently part of large-scale experimental research intent on restoring, and evaluating responses to, late successional forest structures (and contrasting treatments with controls) in eastside pine forests (Oliver and Powers 1998, Zack, and others 1999).

For this study, we wished to evaluate the snag densities in plots not subjected to experimental manipulation. Thus, at BMEF we opted to evaluate snag density at three of four of the existing Research Natural Areas (RNAs) that are part of our study plots. These RNAs had no prior logging history and an 80+ years of history of fire suppression. One RNA—RNA C—was subject to a prescribed fire in 1997. At GAMA, we randomly chose three plots from the 14 plots that, in 1999, had not yet been logged or had a prescribed fire treatment as part of our experimental study there.

The three RNAs at BMEF comprised a total of 284 acres (ca. 115 ha.), while all plots at GAMA are exactly 100 acres in size so the total there was 300 acres (about 40.5 ha.) *(table 1).* All plots at both sites are gridded with spikes and uniquely numbered caps at 100-m intervals.

At each plot at both GAMA and BMEF we mapped and individually tagged (with numbered round aluminum tags nailed on the north side of the snag at dbh height) all snags 20 cm dbh or greater and at least 1 m tall. A given tree was considered a snag if it was dead or clearly dying. Dying trees were detected by the color change in all leaves. In most all cases, the leaf color change was obvious and ranged from yellow to red to brown.

Table 1—*Total snags and acreage at Blacks Mountain Experimental Forest (BMEF) and at the Goosenest Adaptive Management Area (GAMA) sites for those plots assessed Research Natural Areas (RNAs) at BMEF and plot numbers at GAMA. Also noted are the total numbers of "yellow" pine snags (*Pinus ponderosa *and* P. jeffreyi *at BMEF,* P. ponderosa *only at GAMA) for these eastside pine sites.*

	Acres	Snags	S/Acre[1]	Pines[2]	P S/Ac[3]	Percent pine[4]
BMEF						
RNA C	126	389	3.09	259	2.06	66.58
RNA B	91	723	7.95	358	3.93	49.52
RNA D	67	700	10.45	318	4.75	45.43
TOTAL	284	1,812	6.38	935	3.29	51.60
GAMA						
Plot 4	100	181	1.81	46	0.46	25.41
Plot 10	100	245	2.45	72	0.72	29.39
Plot 13	100	186	1.86	24	0.24	12.90
TOTAL	300	612	2.04	142	0.47	23.20

[1] Snags per acre
[2] Total *Pinus* pine snags
[3] Pine snags per acre
[4] Percent of all snags that are pine.

For each snag, we recorded the following information (snag evaluation methods developed by Farris and others 2002): the site (BMEF or GAMA), the plot number or name, the tag number applied to the snag, and the tree species of each snag encountered. For each snag, we measured the diameter at breast height (dbh) in cm and the height to the nearest decimeter (measured with use of clinometers). The condition of the top of the snag (intact, broken, or with multiple leaders) and the color of remaining leaves was recorded. The degree of branching was estimated (from one to four degrees of branching). The percent bark remaining to the nearest 10 percent was recorded for each snag. Bark integrity was judged to be either tight or loose by examination.

The following data were obtained to evaluate the previous history of beetle infestation and woodpecker foraging response. These variables were judged primarily on the snag from diameter-at-breast-height to about 4 meters height. We evaluated and categorized the number of pitch tubes seen, the number of beetle (primarily *Dendroctonus*) exit tubes observed, the number of fungal bodies on the snag observed (primarily *Cryptoporus*), and finally the number of woodpecker foraging sites seen. Each variable was scored into one of five categories: 0 detected, 1-10, 10-20, 20-30, or 30+ detected.

If the snag had bird-excavated cavities, the number was noted. We also noted if the cavity was likely drilled by a woodpecker or by a nuthatch (*Sitta* spp.), which was determined by the size of the hole.

To determine if a given cavity was in use by a breeding bird, we monitored the snag for about 10-minute periods during the breeding season of 1999, as possible. We also used a "Tree-Peeper" extensively. The "Tree-Peeper" is a cavity-examining tool equipped with a small camera lens and light (at BMEF) or with an infrared camera (at GAMA) mounted on a telescoping set of PVC tubing. A small screen for cavity viewing is at the base of the apparatus. The "Tree-Peeper" was able to access almost all cavities up to about 15 m. We believe we detected almost all cavity use by breeding birds in 1999 on our snag plots with these methods in combination, with the likely exception of early season failed nesting efforts. In no case did we examine a cavity thought to have no breeding by the "Tree-Peeper" and find evidence of breeding.

Results

As expected, there were far more snags at BMEF than at GAMA *(table 1).* There are more than three times as many snags (6.38/acre vs. 2.04/acre, respectively) of all tree species at BMEF compared to GAMA overall, and the density of *Pinus* snags represents a sevenfold difference between the sites (3.29 snags/acre at BMEF, 0.47 at GAMA, *table 1).* More than 50 percent of the snags at BMEF were *Pinus*, while less than 25 percent were *Pinus* at GAMA.

There were also dramatic differences in the density of cavities available for cavity-nesting species between the two sites. We counted 0.90 snags with cavities/acre at BMEF compared to 0.42/acre at GAMA, and the total cavities/acre difference was even more pronounced (2.38 vs. 0.56, respectively; *table 2).*

Table 2—*Snag densities with cavities and cavities per acre at BMEF and GAMA.*

	Total snags	Snags with cavities	Snags with cavities per acre	Cavities per acres
BMEF	1,812	257	0.90	2.38
GAMA	612	125	0.42	0.56

We portray the percent of trees with cavities by species for each site in *table 3*. At BMEF, *Pinus* species have cavities more often than either white fir *(Abies concolor)* or incense-cedar *(Calocedrus decurrens).* At GAMA, although *P. ponderosa* has a higher percentage of snags with cavities than the other conifers, the difference between it and white fir is far less pronounced than at BMEF. The proportion of snags designated as "unknown" species is higher at GAMA; we presume most of those snags are indeed very decayed *Pinus* that our crews couldn't discern.

Table 3—*Snags with and without cavities arranged by species. "Yellow"* Pinus *include* P. ponderosa *and* P. jeffreyi.

BMEF	**Snags without cavities**	**Snags with cavities**	**Percent of snags with cavities**
Abies concolor	651	48	6.87
Calocedrus decurrens	99	7	6.60
Yellow *Pinus* spp.	746	189	20.21
Unknown	239	13	5.16
GAMA			
Abies concolor	362	81	18.28
Calocedrus decurrens	1	0	0.00
Pinus lambertiana	13	1	7.14
Pinus ponderosa	97	30	23.62
Unknown	15	11	42.31

The use of snags by cavity-nesting bird species was dramatically different between the sites. Thirty-one cavity-nesting pairs from 10 species were detected at BMEF, while only one pair each of two species were detected at GAMA *(table 4)*. Red-breasted nuthatches *(Sitta canadensis)* (seven pairs), northern flickers *(Colaptes auratus)* (six), and mountain chickadees *(Poecile gambeli)* (five) were the more commonly encountered nesting species at BMEF. Other species included white-breasted nuthatches *(S. carolinensis)* (three pairs found), Williamson's sapsuckers *(Sphyrapicus thyroideus)* (two), and single nesting pairs of American kestrel *(Falco sparvarius),* white-headed woodpecker *(Picoides albolarvatus),* black-backed woodpecker *(P. arcticus),* and brown creeper *(Certhia americana)*. Two nuthatch and one woodpecker species nested but were not identified to species with certainty, and one other cavity-nesting species was not identified at all, but the nest had eggs. Only one nesting pair each of mountain chickadees and red-breasted nuthatch were found at GAMA. This fifteenfold difference is much greater than any measure of snags or cavities reported above. Overall, nesting use as a function of available cavities was surprisingly low (about 12 percent of snags with cavities used at BMEF and only 2 percent at GAMA; *table 4).*

Table 4—*Number of bird pairs nesting, total number of bird species nesting, and relationships to the number of snags and cavities at BMEF and GAMA sites.*

	Total individual nests	**Total number of bird species nesting**	**Nests per snag**	**Nests per snag with at least one cavity**	**Nests per total available cavities**
BMEF	31	10	0.017	0.12	0.05
GAMA	2	2	0.003	0.02	0.01

There was a tendency for cavity-nesting birds to use snags of larger size than snags with cavities overall, and further for cavity-bearing snags to be larger than snags without cavities (with size based on dbh) at BMEF *(fig. 1).* A similar pattern of snags with cavities being larger overall than snags without cavities occurred at GAMA as well *(fig. 2).* At both sites (BMEF and GAMA), the majority of snags are in the most decayed category (decay measured as percent bark remaining) *(fig. 3).*

There are weak tendencies of bark beetle activity and whether the snag has cavities *(table 5).* Recognizing that almost all "0 exit tube" entries come from snags that have no bark and thus the details of bark beetle activity are lost, we found that at both BMEF and GAMA the highest percentage of snags with cavities were those that had the highest counts (31+ exit tubes). More compelling is the fact that 23 out of 28 snags that had the highest beetle exit tube counts had cavity-nesting birds at BMEF. Further, 20/28 snags that had nesting birds had the highest category of woodpecker foraging (31+ woodpecker foraging excavations) on the bark.

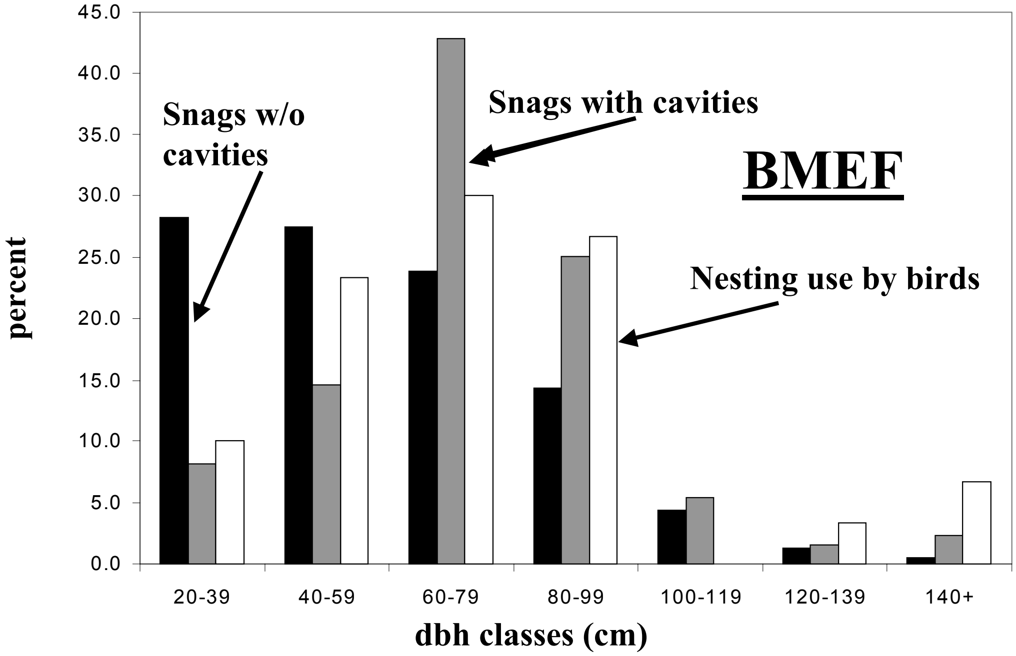

Figure 1—Percent representation of snags without cavities (black bars), snags with cavities (white bars), and snags with cavity-nesting birds (gray bars) as a function of dbh size classes at BMEF.

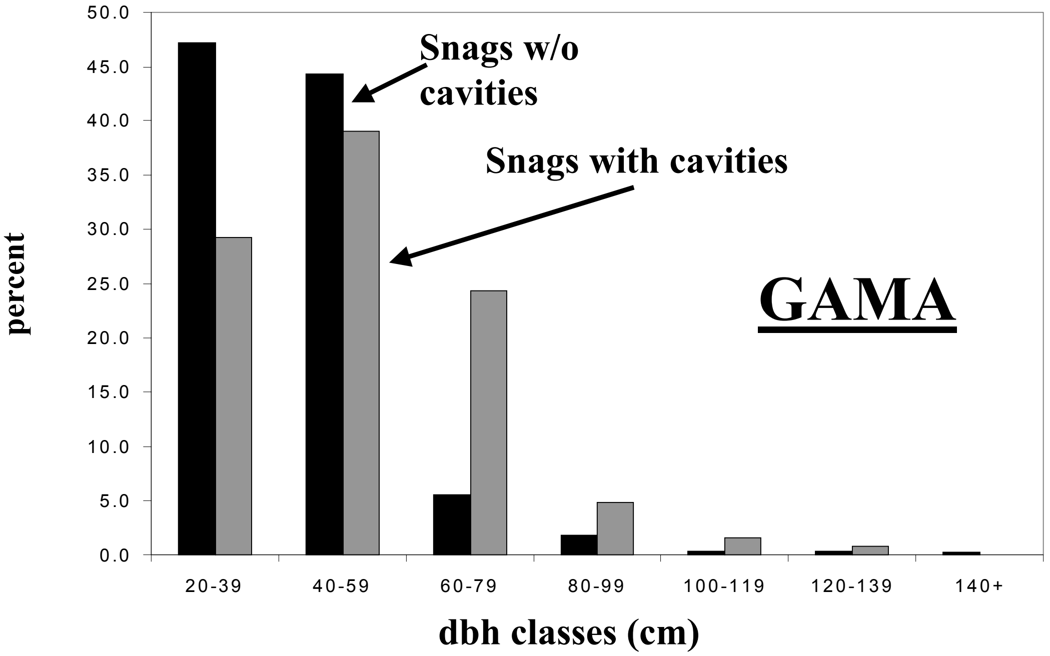

Figure 2—Percent representation of snags without cavities (black bars) and snags with cavities (white bars) at GAMA (cavity-nesting birds [N=2] not represented).

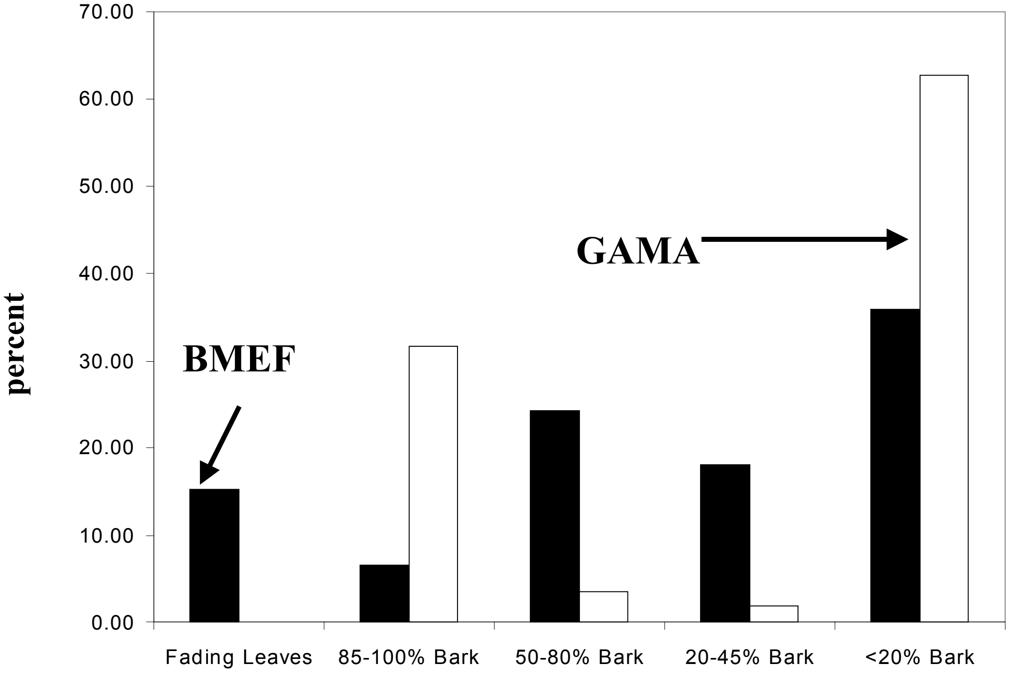

Figure 3—Percent representation of snags in various categories of decay (portrayed as the percent bark remaining) at BMEF (black bars) and at GAMA (white bars).

Table 5—*The relationship between beetle exit tubes detected on a snag and the occurrence of cavities on the snag for BMEF and GAMA.*

BMEF	Total snags	Snags with cavities	Percent of snags with cavities
0 exit tubes[1]	7	7	50.00
1-10 exit tubes	27	4	12.90
11-20 exit tubes	42	7	14.29
21-30 exit tubes	56	11	16.42
31+ exit tubes	624	177	22.10
GAMA			
0 exit tubes[1]	12	8	40.00
1-10 exit tubes	9	3	25.00
11-20 exit tubes	28	5	15.15
21-30 exit tubes	37	8	17.78
31+ exit tubes	24	10	29.41

[1] The “0 exit tubes” category includes snags with no remaining bark, thus no possibility of detecting exit tubes.

Discussion

We initiated this study to begin to quantify what would seem to be straightforward relationships of “snags per acre” and wildlife use. As we previously noted, quantifying and implementing this relationship is an essential element of forest management for wildlife.

For our study, we quantified cavity-nesting bird use of cavities. The use of the “Tree Peeper” would allow us to detect nocturnal small mammal use (none were detected in cavities). As expected, we found strong differences in both snags and cavity-nesting birds between our two sites. At the Blacks Mountain Experimental Forest (BMEF), with a history of little logging and thus large stands of large ponderosa and Jeffrey pine, we found snags at three times the density compared to our Goosenest Adaptive Management Area (GAMA) site, a site with a long history of logging and thus few large trees. The cavity-nesting bird density was even more pronounced, as BMEF had 15 times the nesting pairs as GAMA (31 vs. 2 breeding birds in cavity nests, respectively).

These main results, however, do not afford us a start in enumerating a “snags per acre” prescription in eastside pine forests for several reasons. First and foremost, the majority of *Pinus* snags in the landscape do not have cavities, so simply counting “snags per acre” dramatically underestimates the potential density of cavities for wildlife. In our study, three-fourths or more of yellow pine snags did not have cavities, and this disparity was true for all snag species *(table 3)*. The seeming “requirement” of sapwood decay in yellow pine snags in order for woodpeckers to excavate cavities requires further study. Snag numbers differed dramatically between sites, and so did nesting bird response, but at both sites there were many available cavities unused.

We feel that forest managers may well be asking a misleading question. “Snags per acre” requirements implicitly assume an equilibrium condition and reflect only one ecological requirement for a given cavity-nesting species. Our subsequent discussion will address these concerns and indicate the direction our research is taking as a result.

First, the vanishingly few cavity nesters detected on our GAMA plots is remarkable and suggests strongly that a consideration of foraging habitat and other ecological requirements must be part of the "snags per acre" management considerations. This is an important, but somewhat daunting proposition, as potential cavity-nesting species are diverse, and each species likely has very different foraging ecologies, as well as other differences in habitat requirements. There were an abundant number of unused cavities at both sites (about 88 percent of the cavity-bearing snags were unused at BMEF and 98 percent at GAMA, derived from *table 4),* suggesting that cavity availability is not driving the differences between sites. However, we have no measure of cavity "quality." Thus, we cannot know if unused cavities were for some reason unusable by birds. Their interiors may have been too decayed, or previous use by nesting birds may have fouled the nest environs.

The size of snags does differ between sites, with BMEF having an apparent abundant population of large snags, while GAMA has very few large snags (compare the distributions of snag dbh sizes and proportions in *figs. 2, 3).* As cavity nesters at BMEF used larger snags on average *(fig. 2),* it is possible that one explanation for the dramatic difference in cavity-nesting birds between sites is the presence of large snags available for nesting at BMEF, and their paucity at GAMA, even though excavated cavities are apparently abundant at both. This assertion cannot be a complete explanation, however, because there is wide variation in the height of cavities used *(fig. 2)* at BMEF and in other studies (Bull 1983, Cline and others 1980, Ganey 1999, Laudenslayer this volume, Mannan and others 1980, Miller and Miller 1980, Moorman and others 1999, Raphael and White 1984, Scott 1978). Nonetheless, the loss of large trees due to logging in eastside pine and other forests, over the past century has major implications for cavity-nesting birds.

A consideration of snag "demography" is also important (Bull 1983, Cline and others 1980, Harmon 1982, Huggard 1999, Keen 1955, Moorman and others 1999), as snags do not stand forever in forests, and in eastside pine they may, on the average, fall 8 years after tree death (Landram and others 2002). In our study, the majority of standing snags are very decayed (i.e., have less than 20 percent of their bark remaining; *fig. 3).* This suggests an uneven recruitment of trees into snags, such that it seems possible that the density of snags in our forests is declining. Clearly, forest managers must have a sense of snag recruitment in relationship to snag fall, and the patterns and processes that underlie them, when addressing wildlife needs.

Our results suggest an intriguing connection with biological activity early in the decay process of snags, its relation to a snag's eventual capacity to have cavities, and whether those cavities have nesting birds using them. Our collaborations (Farris and others 2002, Shea and others 2002) suggest that for ponderosa pine, the key to snags containing cavities may lie in the understanding how and if sapwood decay organisms are part of the decay process. In ponderosa pine, it is the sapwood (Rayner and Boddy 1988), not heartwood as in most other conifers, that is the tissue excavated by woodpeckers into nesting cavities. Experimental comparisons between pheromone-baited killed ponderosa pines and girdled pines (Shea and others 2002) reveal that far more cavities have been excavated in trees that were experimentally killed by bark beetles. Those results, and our correlations reported here, suggest that it might be that the action of bark beetle infestation and woodpecker foraging response increases the probability that sapwood decay organisms are part of the decay process, increasing the likelihood that a given snag may later be capable of cavity excavation. As only about 20-24 percent of our pine snags at both sites had cavities *(table 3),* it seems possible that sapwood decay does not occur in the majority of decaying snags.

It is also important to remember that the coupling of fire and bark beetle attack has been dramatically disrupted in the century of fire suppression. In the context of snag ecology, the historical prevalence of frequent, low intensity fires in eastside pine has been altered to infrequent, high intensity fires (Agee 1993, Skinner and Chang 1996), which changes how trees respond (survive or succumb) to fire (see Jackson and others 1999). Our understanding of bark beetles, their natural forest ecology, and rates of infestation (e.g., Christiansen and others 1987, Goyer and others, 1988, Ross and Niwa 1997) is likely incomplete because we rarely have observed the coupling of bark beetle activities in natural fire regimes. Certainly, the response to fires by woodpeckers (Blackford 1955, Koplin 1969) and how that was likely central to their life histories has been dramatically disrupted. These issues are interrelated and were likely historically intertwined in generating historical “snags per acre” levels lost in the past century.

We view the understanding of these complexities to be of primary importance in forest management for wildlife. Our ongoing collaborative research is focused on efforts to reconstruct historic forest structure and fire regimes in eastside pine, evaluate the wildlife and bark beetle responses to prescribed fire, and understand the interactive ecology of snag decay (including bark beetles, woodpeckers, and sapwood decay onset) as it relates to the possibility of cavity excavation. We feel it crucial to understand snags not as entities for simple enumeration (a “snags per acre” prescription), but as the result of complex interactions in dynamic forests. We hope this research pathway affords us a view of how snags develop and proliferate in the eastside pine forest system.

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Distribution Patterns of Birds Associated with Snags in Natural and Managed Eastern Boreal Forests[1]

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Abstract

In boreal forests, several bird species use standing dead trees for feeding or nesting and depend on them for their survival. Studies on wildlife use of snags have shown that their availability is greatly influenced by the age of the forest and the type of perturbation (natural versus anthropogenic). Accordingly, cavity-nesting birds seem largely affected by these changes in availability of snags. In North American boreal forests, relationships between birds and dead wood availability have predominantly been documented in western forests. The dynamics of dead wood and the distribution patterns of birds associated with this habitat feature remain largely unknown in eastern black spruce forests. Distribution patterns of birds associated with dead wood were documented in the eastern black spruce forest of northwestern Quebec, Canada. Study areas were composed of four forest landscapes (50-100 km^2) that were naturally disturbed by different fire events (1 year, 20 years, 100 years and > 200 years) and two logged landscapes (20 years, 80 years). Birds were surveyed by point counts. Overall, 348 point counts were distributed over the six forest landscapes. Vegetation plots centered at each point count were used to sample live trees and dead wood. In naturally disturbed forest landscapes, species richness and abundance cavity-nesting birds reached a peak in early post-fire and in mature forest landscapes. Standing dead wood availability and abundance patterns of cavity-nesting birds were significantly less in 20-year-old managed forests landscapes than in those of naturally disturbed forests landscapes. This pattern was persistent in mature forests comparisons between 80-year-old horse-logged second-growth forests and mature forests of post-fire origin. Our results suggest that old-growth forests in this portion of the eastern black-spruce forest ecosystem do not play a key role for cavity-nesting birds. Mature and over-mature stands are, however, key habitats for many species of secondary cavity nesters, whereas early post-fire stands are key habitats for primary cavity-nesting birds and represent the main source of recruitment for standing dead wood in this ecosystem. Changes in silvicultural practices designed to maintain specific structure of over-mature stands (increased partial cutting) may provide a means for maintaining cavity-nesting birds at the landscape scale. Intensification of salvage cutting in early post-fire landscapes is another serious concern in black spruce forests. Reduction in the overall availability of dead wood through such forest practice may affect populations of some primary cavity nesters that are restricted to this specific forest type.

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Introduction

In the boreal forest ecosystem, large-scale natural disturbances, especially fires, have historically played a major role in determining the structure of boreal forest landscapes (Anglestam 1996, Bergeron 1991, Johnson 1992, Van Wagner 1978). In the last 40 years, however, commercial timber management has become the prevalent perturbation in many parts of the boreal forest (Anglestam 1996, Enoksson and others 1995, Franklin and Forman 1987, Spies and others 1994). Although forest management may show some similarities with natural disturbances (fire and insect outbreaks) to which organisms are adapted, there are important differences between these two types of disturbances. Cutting rates are generally shorter than natural disturbance cycles (Gauthier and others 1996, Spies and others 1994) and more severe in terms of live trees and coarse woody debris that remain after logging (Spies and others 1994). Hence, in industrial forest landscapes, concerns regarding the issue of biodiversity have identified two important aspects: changes in the age structure of forests, and whether managed forests successfully substitute for unmanaged forests for maintaining biodiversity (Franklin 1993, Hansen and others 1991, Hejl and others 1995)—particularly in their capacity to maintain key environmental attributes such as coarse woody debris.

Until now, most knowledge on forest ecosystems biodiversity and how it relates to key habitats such as over-mature and old-growth stand types or key stand attributes such as density and quality of standing dead wood and fallen logs has mainly come from studies conducted in the Pacific Northwest forest (Hansen and others 1991, 1995a,b; Lamberson and others 1992; McGarrigle and McComb 1995; Spies and others 1988). Recommendations and management guidelines for sustainable forestry in this biome are not necessarily applicable in the eastern boreal forest. Moreover, as noticed by Freedman and others (1994), the status of forest types (by age-class) in eastern Canada and their contribution to biodiversity across landscapes remains poorly documented. Comprehensive efforts to assess the state of forest types and their contribution to biodiversity in the eastern boreal forest are critical. Coincident with these efforts, the question of how well managed forests substitute for natural forests is linked to quantitative field investigations that focus on whether key differences exist in biodiversity patterns between managed forests and naturally disturbed forests, and on how critical these differences are to the maintenance of regional biodiversity. For instance, in the eastern boreal black spruce forest, comparatively little information exists on responses of birds associated with dead wood. Does the general pattern of increased structural complexity of the forest as it is aging still hold for landscapes dominated by black spruce stands? Do the quantity and quality of dead wood show the same patterns of variation with forest age that has been documented in western coniferous forests? How do birds respond to changes in dead wood availability across time? Even though it is well recognized that standing dead wood is far less abundant in forests that were logged than they are in forests that regenerate from fire, what is the magnitude of differences in density of snags and in bird species' abundance? To tackle these issues, ecological investigations must incorporate both stand and landscape level approaches (Freedman and others 1994, Hejl and others 1995, Thompson and others 1995).

In this paper, we document distribution patterns of birds associated with snags in the eastern black spruce forest of northwestern Quebec, Canada. We examine abundance patterns across broad gradients in forest age and management history in four forest landscapes (50-100 km^2) that were naturally disturbed by different fire events (1 year, 20 years, 100 years and > 200 years) and in two timber harvested landscapes (20 years, 80 years). The first objective of this study is to document and explain the distribution patterns of birds associated with standing dead wood in naturally disturbed forest landscapes. The second objective is to evaluate some of the effects of forest management on this avian guild by comparing bird patterns and standing dead wood availability between natural and managed forest landscapes.

Study Area

The study was undertaken in the eastern black spruce forest in the northwestern part of the Abitibi region in Québec (49°13'17" to 49°51'05"; 78°38'35" to 79°23'13") and in the Abitibi Lake Model Forest (49°03'33" to 49°42'20"; 80°09'03" to 80°38'35") in Ontario *(fig. 1).* These regions are part of the northern Clay Belt, a broad physiographic unit characterized by lacustrine deposits from the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Clay soils are predominant in the region, the topography is relatively flat, and the forest mosaic is dominated by stands of black spruce *(Picea mariana).* Jack pine *(Pinus banksiana)* is dominant on drier sites such as outwash deposits, old beaches, and eskers (Rowe 1972).

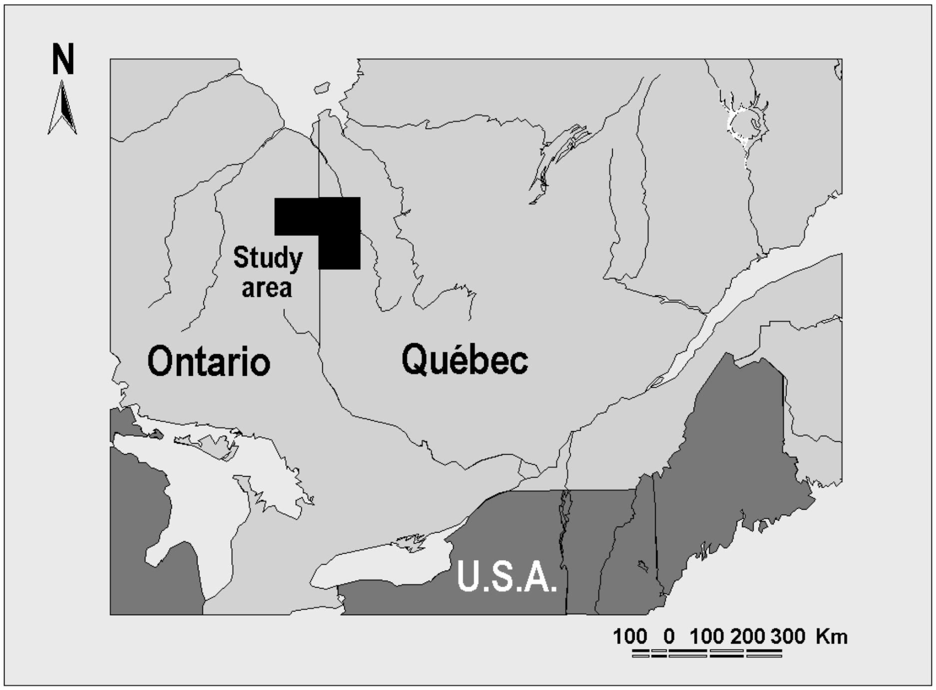

Figure 1—Location of the study area in the Quebec-Ontario eastern boreal black spruce forest.

Even though industrial forestry is increasingly shaping the present forest landscape, a large proportion of the forest cover is under a natural disturbance regime. Dendrochronological reconstructions of fire events indicate that natural fire frequency has decreased in the last 150 years (Bergeron and others 1998, 1999b). This decrease is responsible for the presence of large tracks of over-mature and old-growth forests in the study region. For the Quebec section of our study area, industrial timber harvesting was initiated in the early 1970s, whereas even-aged management is the dominant silvicultural system with clearcutting as the main forestry practice. In Ontario, some areas have been horse-logged in the 1920s. As in many other regions of the Canadian boreal forest, clearcutting is followed by planting and seeding in 20 percent of the area, whereas 80 percent of logged areas are under natural regeneration (Haddon 1997).

Methods

Study Design

Our study sites were within an area where a large (25,000 km^2) fire history reconstruction project has been ongoing between the 48th and the 50th degrees of latitude along a south-north transect (Bergeron and others 1999b). A stand initiation map at the scale of 1:250,000 was constructed using either archives and aerial photographs (some dating from the 1930s) to delineate fires during the 20th century, or dendrochronology records of cored trees for older fires. We used forest cover maps and the fire history reconstruction map by Bergeron and others (2001) to delineate six forest landscapes (100 to 250 km^2) that originated from different fire events (1 year, 20 years, 100 years and > 200 years) or logging events (20 years clear-cut and 80 years horse-logged). The forest cover maps and aerial photographs (for horse-logged forests) allowed us to identify the location of timber harvested areas, the time when they were harvested, and the location of access roads.

In each landscape, sampling stations were grouped by line transects to maximize time spent sampling, minimize time traveling between sites, and include inter-stand heterogeneity of forest mosaics. Four to six stations were located along line transects 1.2 to 2.5 km long. Line transects were separated by at least 1 km. Distance between stations varied from 350 to 450 m ensuring independence between stations (Bibby and others 1992). Each station was within a relatively homogeneous black spruce forest type. Overall, 348 sampling stations along 80 line transects provided extensive coverage of the study area.

Bird Sampling

The point count method was used to sample bird populations at each sampling station (Blondel and others 1970, 1981, Ralph and others 1995). Sampling was initiated at dawn and was conducted until 9:00 (EST). Data on bird species occurrence and abundance were recorded within a fixed radius of 75 m and over an unlimited distance around each station. Sampling stations were visited twice during the breeding season of 1997 and 1998: once in the first half and once in the second half of June. On each visit, birds (seen or heard) were recorded at 5-min intervals for a 20-min period. The sampling sequence varied so that each station was visited once at dawn and once later in the morning to maximize detection probabilities of each species present.

Sampling procedure adopted in this study with regard to the number of visits, the spacing of visits during the breeding season, the hourly periods appropriate for sampling, and count duration were based on a methodological study on the efficiency of the point count method in characterizing bird communities (Drapeau and others 1999a). The maximum count on either one of the two visits was used to estimate the relative abundance of each species at each station. Bird censuses were conducted in comparable weather conditions, under clear and partly cloudy sky, and when wind speed generally did not exceed 8 km per hour. Counts were interrupted when wind speed exceeded 16 km per hour and when raining. Each sampling station was visited in only 1 of the 2 years.

Habitat Variables

Habitat measurements were centered on the bird sampling station. From mid-July to mid-August of each year, features of vegetation structure and composition of live trees and dead wood were measured at each sampling station within a single triangular plot of 40 m per side covering a sampled area of 700 m^2. For dead wood, measures of both standing dead wood and fallen logs were recorded in each plot. In this paper, emphasis is put on relationships between birds and standing dead wood. Hence, only methods for snags are presented.

Diameter at breast height (DBH) was recorded for all standing dead trees (snags) > 1.3 m tall in all plots. For each snag, decay stage was recorded using three variables: crown condition, bark, and wood condition. Crown condition was estimated by using the following classes: (1) all foliage, twigs and branches present; (2) some or all foliage lost, possibly some twigs lost, all branches usually present, possible broken top; (3) no foliage, up to 50 percent of twigs lost, most branches present, possible broken top; (4) no foliage, up to 50 percent of branches lost, top usually broken; (5) most branches gone, some sound branch stubs remain, top broken; (6) no branches, some sound and rotting branch stubs, top broken; and (7) no branches, minimum of rotting branch stubs, top broken.

Bark retention was determined using the following classes: (1) all bark present, (2) 1-5 percent bark lost, (3) 5-25 percent bark lost, (4) 26-50 percent bark lost, (5) 51-75 percent bark lost, and (6) >76 percent bark lost. Wood condition was assessed as follows: (1) no decay, (2) probable limited internal decay and wood essentially hard, limited decay, (3) wood mostly hard but decay spreading, soft wood present (4) balance of hard and soft wood (5) more soft wood than hard wood, (6) no more hard wood, and (7) hollow shell. Wildlife tree use, i.e., feeding activities (small holes and/or bark flaking) and nesting activities (nesting cavities) were also recorded for each of snag. These marks were identified to the bird species when possible.

Data Analyses

To assess the overall stage of decay of standing dead wood, we used principal components analysis (PCA) (Legendre and Legendre 1998) to derive a single component variable that best describes the decomposition stage of each snag and that can provide a quantitative value of the mean stage of decay of snags in each sampling station. The first principal component accounted for 69 percent of the variance of the set of decay variables. PCA1 was partitioned into three equidistant classes of decay that will be used in further analyses.

Comparisons among landscapes were conducted for species groups, such as (1) all cavity-nesting birds, (2) primary, and (3) secondary cavity-nesters. Species were grouped on the basis of their ability to excavate trees or to use holes excavated by other species. Relationships between these species groups and forest landscape types were determined using Kruskal-Wallis tests (Sokal and Rohlf 1981).

Differences between forest landscapes in mean availability (basal area) and decay stages of snags were evaluated using Kruskal-Wallis tests. For all significant Kruskal-Wallis tests, a Student-Newman-Keuls's (SNK) pairwise comparison procedure was used *a posteriori* to determine which landscapes showed significant differences. All analysis were performed using SAS (SAS Institute Inc. 1990). The significance level of each test was 0.05. Even though we counted birds with both limited (75 m radius) and unlimited distance (> 75 m) count points, data analyses were performed only with birds registered within 75 m of sampling stations centers.

Results

Habitat Distribution of Birds at the Guild Level

Overall, 94 species were detected across the 348 sampling stations. Half of these species were uncommon; 52 were detected in more than 5 percent of the sampling stations. Across landscapes the ratio of species associated with standing dead wood for nesting and feeding (hereafter cavity-nesting birds, CNB) peaked at 15 percent. Along the gradient of time since fire, CNB's reached a peak in early post-fire forests and in the mature forest landscape *(fig. 2).* The ratio of primary cavity nesters (PCNB) was highest in the early post-fire landscape, whereas the ratio of secondary cavity nesters (SCNB) peaked in the mature forest landscape, but was also important in old-growth forests. PCNB birds were absent in the old-growth forest landscape.

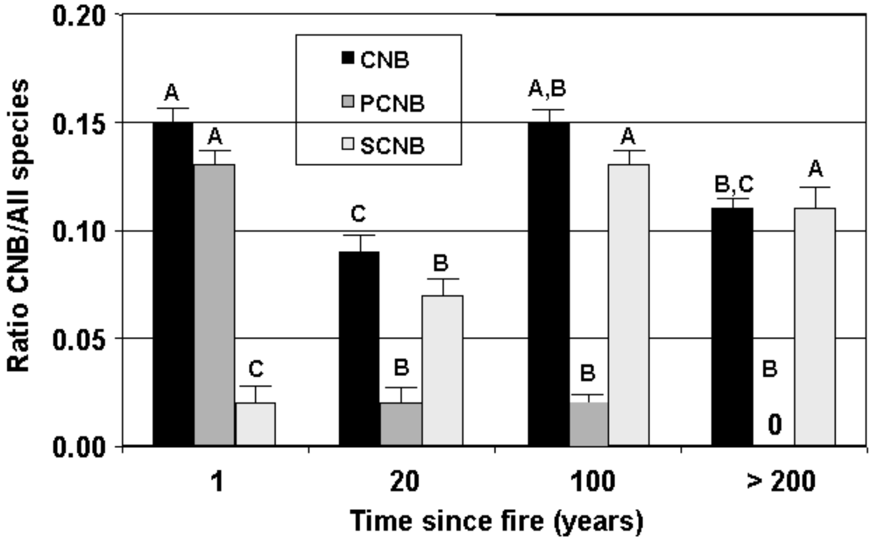

Figure 2—Distribution of cavity-nesting birds (CNB), primary cavity nesters (PCNB) and secondary cavity nesters (SCNB) in four natural landscapes that cover a time since fire gradient from early post-fire to old-growth forest types in the eastern boreal black spruce forest in Abitibi, Québec. For each category of birds, significant differences (*P* < 0.05) for mean values (± 1 SE) between landscapes are indicated by different letters.

Changes in Standing Dead Wood over Time since Fire

Significant differences in standing dead wood availability were observed among forest landscapes *(fig. 3)*. Availability of snags was highest in the 1-year post-burned forest landscape and was lowest in the old-growth forest landscape *(fig. 3)*. Landscapes burned 20 years and 100 years (mature forests) were similar with intermediate values.

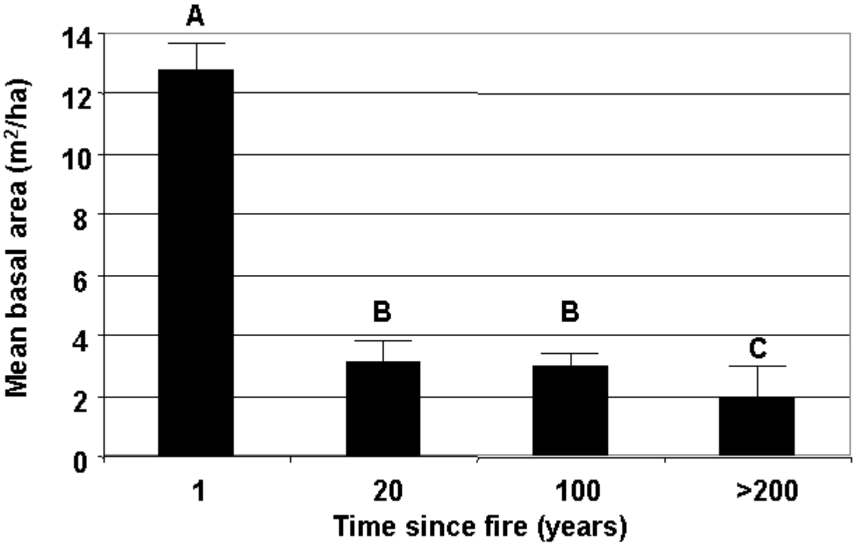

Figure 3—Changes in availability of standing dead wood in relation to forest landscapes' time since last fire in the eastern boreal black spruce forest in Abitibi, Québec. Significant differences (P < 0.05) for mean values (± 1 SE) among landscapes are indicated by different letters.

The decomposition stage of snags varied significantly among forest landscapes (Kruskal-Wallis: $\chi^2 = 27.7$, df = 3, $P = 0.001$). The majority of standing dead trees were scarcely decayed in the early post-fire landscape, whereas the 20-year burned landscape showed the highest proportion of highly decayed snags *(fig. 4)*. Decay stages of dead trees were similar between the mature and the old-growth forest landscapes. In these landscapes, the largest proportion of standing dead trees were in the intermediate decay class *(fig. 4)*.

Birds and Dead Wood in Managed Forests

Comparisons between managed and natural forest landscapes were conducted for two time periods: 20 years after disturbance and 80 to 100 years after disturbance. Mean basal areas of snags > 5 cm were significantly higher in both 20 and 100 year post-burned landscapes than in logged forests *(fig. 5a)*. The proportion of birds associated to snags was also higher in post-burned landscapes than in their logged counterpart for both time periods (20 years and > 80 years after disturbance). The only comparison that showed no significant difference was with the proportion of primary cavity nesters in the 20-year-old logged and burned landscapes *(fig. 5b)*.

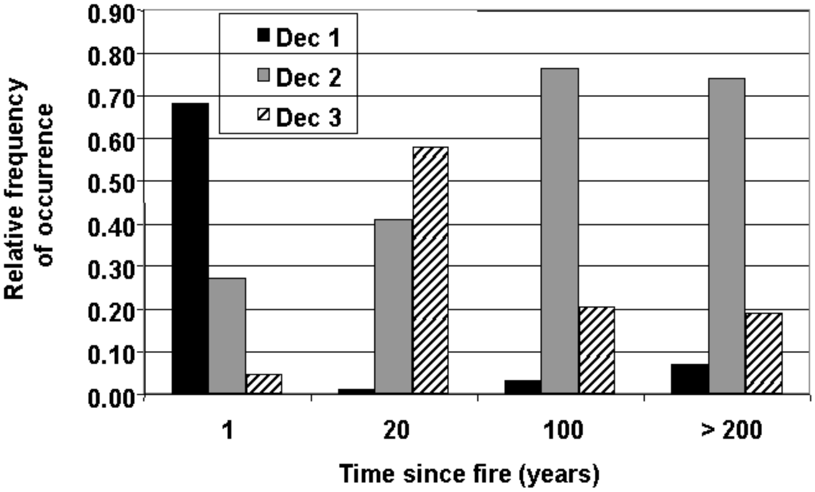

Figure 4—Decay stage of standing dead wood in relation to forest landscapes' time since last fire in the eastern boreal black spruce forest in Abitibi, Québec. Decay classes (Dec 1= weakly decayed, Dec 2= intermediate, Dec 3= highly decayed) were derived using scores on the first axis of a PCA conducted on the set of decay variables for standing dead trees.

Discussion

Old-growth forests are usually considered key habitats for wildlife due to the overall increase in complexity of forest structure, amount of dead wood, and increases in live and dead tree diameter (Probst and others 1992, Raphael and White 1984). Our results show that in the black spruce forest, this age-class type does not have the same importance in the distribution of birds associated with dead wood than what has been suggested by other studies. For instance, no primary cavity-nesting birds were detected in the old-growth forest landscape, and the importance of secondary cavity-nesting birds in these forests was mainly related to Winter Wren's *(Troglodytes troglodytes)* abundance, which in our study area was widespread across the age-class gradient sampled (Drapeau and others 1999b). Coincident with these results, data on the mean basal area of snags was at its lowest in the old-growth forest landscape. Thus, snag availability was significantly reduced in old-growth forests, in particular for the larger snags (>15 cm dbh) that are significantly more likely to show evidence of feeding and nesting use by birds (Hutto 1995, Nappi 2000) than are smaller trees. This may explain why primary nesting birds were absent in the old-growth landscape. Our results suggest that old-growth forests in this portion of the boreal forest ecosystem may not play a key role for cavity-nesting birds. This is contrary to Shieck and others (1995) findings on the importance of old-growth stands for birds that nest in tree cavities in aspen-dominated boreal forests in Alberta. The importance of old-growth forests for birds may change depending on forest ecosystem or geographic area. In a recent review on silviculture and Rocky Mountain forest birds, Hejl and others (1995) found that assigning species as old-growth associates is not an easy task. They also found that even though some species were more abundant in some old-growth forests of the Rocky Mountains, none of these species were consistently more abundant in all old-growth forests among the studies they compared.

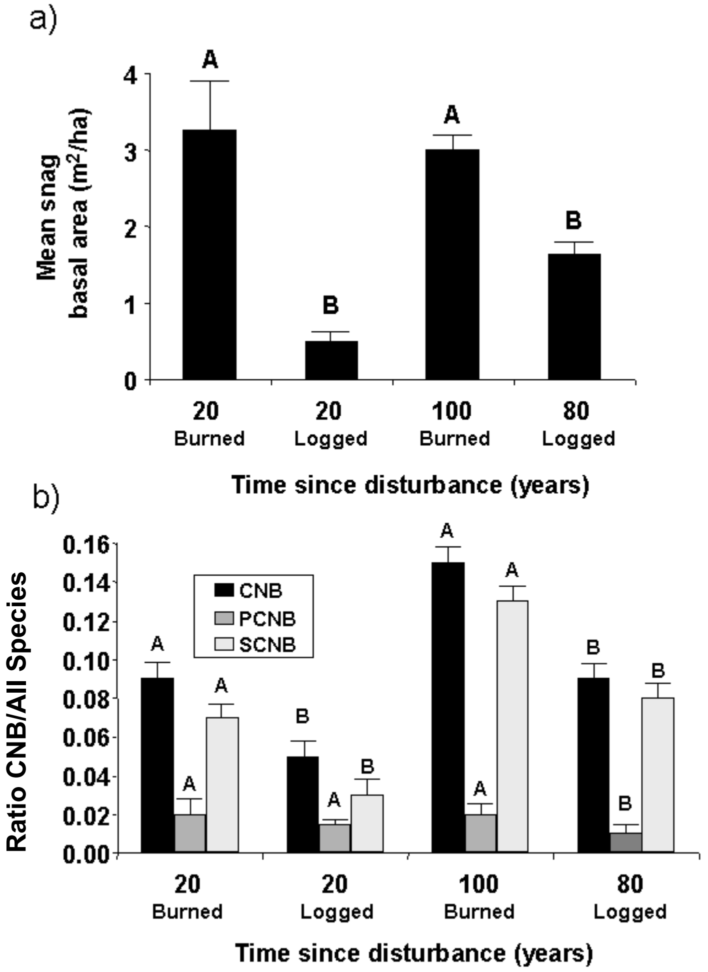

Figure 5—Distribution of (a) standing dead wood and (b) cavity-nesting birds in post-logged and post-burned forests in the eastern boreal black spruce forest in Abitibi, Québec. Significant differences ($P < 0.05$) between means (± 1 SE) for combinations of age-related harvested and naturally disturbed landscapes are indicated by different letters.

Comparisons among all four natural forest landscapes showed highest occurrence of primary cavity nesters (woodpeckers) and secondary cavity nesters in recently-burned forests and mature to over-mature stands, respectively. In early post-fire forests some species, like the black-backed woodpecker *(Picoides arcticus),* were not only more abundant but were restricted in their habitat distribution (Nappi 2000). Distribution of this woodpecker species in eastern boreal forests is thus consistent with Hutto's (1995) and Saab and others (1998) results in northern Rocky Mountain coniferous forests. Across their range, black-backed woodpeckers seem to be specialists of recently burned forests. The abundance of secondary cavity nesters reached its peak in mature to over-mature forests possibly because this age-class had a higher density of large live trees (> 20 cm) with few large snags, which may provide the combination of habitat characteristics that is important for species like the red-breasted nuthatch *(Sitta canadensis),* the brown creeper *(Certhia americana),* and the boreal chickadee *(Poecile hudsonicus).*

Quantity and quality of standing dead trees also indicate that early post-fire forests are key habitats for snag recruitment. This is not surprising in boreal systems where trees killed by fire is clearly a major source of dead wood. The importance of recently burned forests in our study area is, however, exacerbated by the fact that, in contrast to other forest ecosystems, the basal area or snags did not increase in our old-growth forests but was significantly less than in mature forests (Clark and others 1998, Tyrrell and Crow 1994).

Comparisons between logged and burned forest landscapes suggest that even though the availability of snags is low in natural landscapes at these time periods (20 and 100 years), clearcutting is not only significantly reducing the amount of snags but also the proportion of cavity-nesting birds. Secondary cavity nesters are particularly reduced in these forest age-classes. Retention of snags and living trees in black spruce forests during timber operations should be given more attention in future managed landscapes.

Management Implications

Although forest management's main objective is to perpetuate forests not to convert them to other land uses as with other human disturbances (Hejl and others 1995), it may nevertheless alter the composition and structure of forest mosaics and hence biodiversity in the long term. In eastern boreal mixed-wood forests, large-scale conversion of mature forests from mixed-wood to deciduous cover due to the impacts of industrial logging on vegetation regeneration (Carleton and McLellan 1994) coupled with short timber rotations (Spies and others 1994, Gauthier and others 1996) may jeopardize the ecological integrity of bird communities (Drapeau and others 2000). In the black spruce forest, even though tree species composition will not be affected by short rotations, changes in the structural complexity are expected, notably in the overall decrease of over-mature and old-growth forests (Bergeron and others 1999a). Although our results are not consistent with those of other studies as for the importance of old-growth forests for cavity-nesting birds, they nevertheless raise concerns on the future of mature and over-mature stands that are key habitats for many species of secondary cavity nesters. For our study area, Bergeron and others (1999a) have showed that the natural forest stand age distribution follows a negative exponential with over 23 percent of the stands in intermediate stage (between 100–200 years). Hence, even though old-growth forests are not as important for birds as they are in other forest biomes, the dramatic reduction in the proportion of intermediate-aged seral stages in black spruce forests under normal rotations may pose a serious threat to bird communities.

Changes in bird communities we observed may be attenuated, provided that current forestry practices are modified in managed forest landscapes. The use of silvicultural practices designed to maintain specific structure of intermediate-aged stands may provide a means for maintaining species of secondary cavity nesters. For instance, diversified forest practices including partial cutting and careful logging that simulates the natural evolution of over-mature black spruce stands could be used to maintain an equivalent proportion of forests stands that retain intermediate-aged stand characteristics across the landscape (Bergeron and others 1999a).

Finally, given the major contribution of recently burned forests, both as a key habitat for primary cavity-nesting birds and as the main source of recruitment for dead wood, the intensification of salvage cutting raises serious concerns in black spruce forests. It not only may compromise the maintenance of viable populations for species that require this specific forest type, but it may reduce the overall availability of dead wood to wildlife across current and future landscapes.

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Habitat Preferences of Primary Cavity Excavators in Washington's East Cascades[1]

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Abstract

Primary cavity excavator (PCE) bird densities and habitat preferences in relation to forest management treatments and snag characteristics were investigated in grand fir forests of eastern Washington. PCE birds selected large diameter, broken top snags for feeding and nesting. They selected western larch and Douglas-fir for feeding excavations and ponderosa pine and Douglas-fir for nest cavity snags. Grand fir were also utilized as available on managed plots. Soft snags with advanced wood decay were particularly important for nest sites. Species composition of PCE birds varied significantly in different forest management treatments, with unique species groups associated with unmanaged and heavily managed sites. Total population densities of PCE birds were most closely associated with snag density, particularly large diameter snags (> 25 cm DBH).

Introduction

Dead wood, particularly standing dead trees (snags) or down logs, is important habitat for many species in forest ecosystems. Primary cavity excavator (PCE) birds, best represented by woodpeckers, use this dead wood extensively. These species excavate hollow cavities in tree stems, usually in dead and decayed wood, as a part of regular nesting and courtship behavior. These cavities are critical for life history needs of other species of birds and mammals, known as secondary cavity users. Thus, PCE birds can be considered "keystone species" in forest ecosystems, because many other species of forest wildlife are dependent on them for cavities (Wilson 1992).

Characterizing snags selected by PCE birds in any given forest type can provide important basic information for biologists and land managers. This information was unavailable for grand fir *(Abies grandis)* stands in Washington's East Cascades, a major vegetation type in this region, prior to the initiation of our project.

Previous research suggests that important attributes of snags selected by PCE birds in coniferous forests of the western United States include large diameters, advanced decay, and broken tops (Raphael and White 1984, Zarnowitz and Manuwal 1985). Snag abundance has been hypothesized as a limiting factor for PCE populations. A model for predicting "potential population" levels of cavity

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excavating birds based upon numbers of available snags and nesting territory sizes (Thomas and others 1979) has been used extensively as a forest management guideline in the Pacific Northwest. This model assumes a direct relationship between PCE bird and snag abundance. Our study examined the relationship between snags and PCE bird densities in grand fir forests.

Questions we sought to answer with our study included: 1) What are the characteristics of snags selected by PCE birds for feeding and nest cavity excavation? 2) How does PCE species composition and abundance differ among forest management treatments? 3) What habitat variables best predict the abundance of PCE birds across a series of forest management treatments?

Methods

The research was conducted 6 km south of Cle Elum, Washington, in and adjacent to the central portions of the Taneum Creek basin *(fig. 1).* Lands in the study area are owned and managed either by the USDA Forest Service or the Plum Creek Timber Company. Forest conditions in this basin range from recent clearcuts to late-seral mixed-conifer stands.

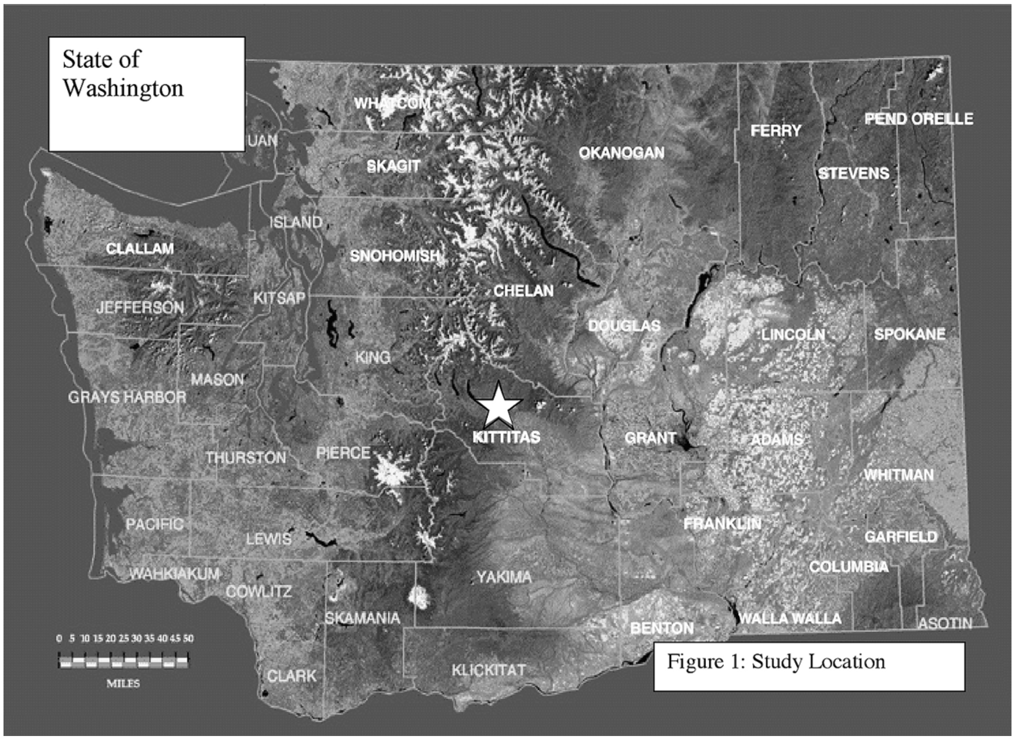

Figure 1—Study location.

Forest Management Treatments

Three plots—Gooseberry, North Fork, and South Fork—were characterized as unmanaged forest habitats. There was no evidence or record of historic logging activity on these sites. Unmanaged stands had heterogeneous overstories of large Douglas-fir and western larch, with understories of predominantly grand fir. Patches of even-aged co-dominant lodgepole pine and Douglas-fir also occurred. These areas were structurally heterogenous due to past fires and other natural disturbances.

Two plots, Taneum and Tillman, were characterized as dense shelterwood habitats where recent logging removed most of the dominant overstory trees and thinned the remaining co-dominant trees between 1983 and 1987. Canopy closure remained high. The residual stand consisted of predominantly Douglas-fir, in a moderately dense stand with high canopy closure. These stands were considerably denser than typical shelterwood treatments.

Two plots, Frosty and Currant, were characterized as seed tree habitats where only a few dispersed, large Douglas-fir or western larch trees were retained after harvest. At the time of this study, the planted understory trees (Douglas-fir and larch) were less than 1 m tall, and the shrub layer was poorly developed. Grazing by domestic sheep had minimized the shrub and herbaceous layers as well. These plots were also logged between 1983 and 1987.

Plot Description

Six 15 ha and one 12 ha rectangular plots were established and sampled for habitat characteristics and PCE birds in 1991 and 1992. The 12 ha plot (Tillman) was the best available replicate of the dense shelterwood treatment. Plots were located in interior portions of large, homogenous blocks of habitat, at least 50 m from substantially different adjacent habitats. A 50 x 50 m grid was established on each plot to facilitate bird and habitat measurements.

Plots were verified as occurring within *Abies grandis* vegetation associations by using the guide, *Forested Plant Associations for the Wenatchee National Forest* (Williams and Smith 1990). All plots had a predominantly north aspect and occupied mid- to upper slope positions. All plots possessed moderate slopes and were within 350 m elevation to each other. One habitat point was measured on each ha of each study plot. Nine habitat parameters were measured on each habitat point: slope, aspect, canopy closure, live tree basal area, live tree density, snag density, live tree and snag species composition, snags selected for feeding and/or nest cavity excavation, and down wood. Slope and aspect were measured with clinometer and compass, respectively. Canopy closure was taken with a spherical densiometer. Live tree basal area was measured with a relaskop or prism. Live tree density and species composition were taken using the point quarter method (Brewer and McCann 1982) at each habitat point. Down wood was tallied using a (Brown 1974) point intercept method to the estimate the approximate tons/acre of dead wood.

All snags were tallied on 20 x 200 m (1 acre) strips within the larger rectangular study plots, at a rate of 16 percent of the total plot area. These strips were systematically located along bird transect lines on the 50 m plot grid. A snag was defined as a standing dead tree with a minimum diameter breast height (DBH) of 10 cm and a minimum total height of 2 m. This definition was based on minimum nest tree diameters and heights for chickadees, the smallest excavator species group observed in the study area (Thomas and others 1979). Recorded for each snag were tree species, DBH, total height, decay class, presence of feeding excavations, presence of nest cavities, and presence of broken tops. Decay Class was recorded using a system developed by Cline and others (1977) using five stages, or Classes, of dead wood decay. Decay Class 5 was eliminated in 1992 surveys and subsequent analyses after 1991 data indicated that very few snags were described in this category. Heavily decayed (Class 5) snags were then described as Class 4. Diameter classes for snag densities were derived from minimum nest tree diameters required for three dominant PCE bird species occurring on this study area: mountain chickadee, hairy woodpecker, and pileated woodpecker (Thomas and others 1979).

Feeding excavations were considered present when the surface of the snag had obvious shallow holes chipped into it by woodpeckers (Mannan and others 1980, Swallow and others 1988). Nest and roost cavity excavations were identified by the presence of much larger circular or oval openings excavated by PCE birds (Horton and Mannan 1988, Mannan and others 1980). We increased the sample size for snags with visible nest cavities by measuring cavity excavated snags and active PCE nests from similar forest habitats within and adjacent to the study plots. No snag included in the data set was more than 150 m from a plot, or in a substantially different habitat from the nearby plot.

Data on PCE bird abundance and species composition was collected on 100 m wide fixed-width transects (Manuwal and Carey 1991) by the first author and a field assistant working alone on each survey. Surveys began before 7 a.m. and were completed by 9 a.m. Time spent on each survey was standardized. Bird censuses occurred in June-July 1991 and May-July 1992. Results were pooled from both years for analyses.

Data were analyzed with Statistical Analysis System (SAS) software. DBH and height of snags with and without excavations were compared using T-tests. Decay class, species, and broken top selection were investigated using X^2 and Kolmogorov-Smirnof tests. Selection for individual categories was examined with two category X^2 tests with Yate's correction (Sokal and Rolf 1969). Species composition of PCE birds was examined using Duncan’s multiple range test, which identifies significant groupings among categorical data. Multiple regression analyses were used to determine which habitat variables were the strongest predictors of bird densities.

Results

PCE Bird Species Observed and Plot Characteristics

Ten species of PCE birds were observed on the study plots *(table 1).* Red-breasted nuthatch, chestnut-backed chickadee, mountain chickadee, and northern flicker were the most abundant species observed. Three-toed woodpeckers were detected only in unmanaged stands.

Basal area and canopy closure varied by treatment, with some significant variation (ANOVA results p=.05) within treatments. Live tree densities varied between treatments, with highest densities on the unmanaged plots. Dense shelterwoods had larger trees removed by logging, but maintained high densities of smaller trees and seed tree plots had few live trees *(table 2).* Six plots had Douglas-fir as the dominant live tree species. On the unmanaged Gooseberry plot, grand fir was the dominant species. Snag density varied across the plots, with the highest densities occurring on two unmanaged plots. The dense shelterwoods and one unmanaged plot had intermediate snag densities. The seed tree plots had the lowest snag densities *(table 3).*

Snag Habitat Selection by PCE birds

Snag selection by PCE birds for feeding and cavity excavation was investigated by analyzing the total sample of 1,638 snags and appropriate subsets. Five snag attributes were analyzed: DBH, height, Decay Class, snag species, and presence or absence of a broken top. Additionally, 40 snags containing active PCE nests were measured and compared with selection characteristics of snags with cavity excavations but without known active nests.

Table 1—*Primary cavity excavator bird species observed on study plots.*

Common name	Abbreviation	Scientific name
Red breasted nuthatch	RBNU	*Sitta canadensis*
Chestnut-backed chickadee	CHCH	*Poecita rufescens*
Mountain chickadee	MOCH	*Poecita gambeli*
Pileated woodpecker	PIWO	*Dryocopus pileatus*
Hairy woodpecker	HAWO	*Picoides villosus*
Black-backed woodpecker	BLWO	*Picoides arcticus*
Three-toed woodpecker	TTWO	*Picoides tridactylus*
Red-naped sapsucker	RNSA	*Syphrapicus nuchalis*
Williamson's sapsucker	WISA	*Syphrapicus thyroideus*
Northern flicker	NOFL	*Colaptes auratus*

Table 2—*Live tree plot characteristics.*

Treatment and plot[1]	Mean Pct canopy	Live tree Basal area M^2/ha	Live tree density > 25 cm DBH/ ha
Unmg			
Goo	89.3	17.6	179.9
SFk	77.6	12.9	175.3
NFk	86.2	18.3	277.8
Dshr			
Tan	64.6	9.9	119.1
Til	75.0	14.6	214.4
Seed			
Fro	8.0	.9	6.7
Cur	2.2	.3	4.9

[1] Treatment: Unmg = Unmanaged, Dshr = Dense Shelterwood, Seed = Seed Tree
Plot names: Goo = Gooseberry, SFk = South Fork, NFk = North Fork, Tan = Taneum, Til = Tillman, Fro = Frosty, Cur = Currant

Table 3—*Snag density/ha by diameter class.*

Treatment and plot[1]	Density/ha by diameter classes (cm DBH)				
	10-25	25-50	>50+	>25	total >10
Unmg					
Goo	88.5	48.5	20.6	69.1	157.6
SFk	113.9	42.4	9.5	51.8	165.8
NFk	78.2	19.7	2.0	21.8	100.0
Dshr					
Tan	58.0	20.2	.8	20.6	77.7
Til	67.9	15.4	1.0	16.5	84.4
Seed					
Fro	14.4	2.9	3.7	6.6	21.0
Cur	5.8	3.3	3.7	7.0	12.7

[1] Treatment: Unmg = Unmanaged, Dshr = Dense Shelterwood, Seed = Seed Tree; see *table 2* for plots.

Characteristics of Feeding Snags

The mean DBH for 677 feeding snags (ave. = 29.3 cm, $p < .0001$) was significantly larger than mean DBH of snags without feeding excavations (n = 775, ave. = 16.7 cm; T-test, $p < .0001$). Feeding snags were also significantly taller (ave. = 14.3 m) than non-excavated snags (ave. = 11.7 m; T-test, $p < .0001$).

Selection of tree species used for feeding snags was found when utilized snags were compared to the total snag sample. Grand fir (X^2, $p = .05$) and lodgepole pine (X^2, $p < .005$) were selected against, while selection for Western larch (X^2, $p < .005$) was found. Douglas-fir and ponderosa pine were neutral for feeding selection. Broken top snags were significantly selected for feeding (X^2, $p < .005$). Preferred characteristics of feeding snags therefore were: large DBH (>25 cm), tall (> 10 m) western larch snag, , with a broken top.

Characteristics of Cavity Snags

It was not known what PCE bird species were responsible for excavating the observed cavities. Mean diameters of cavity and non-cavity snags were compared. Mean diameters of cavity snags (n = 239, ave. = 47.9 cm) were significantly larger than that of non-selected snags (n = 1,399, ave. = 21.9 cm; T-test, $p < .001$) *(table 4).* Heights of cavity snags (ave. = 9.8 m) were significantly shorter than height of snags without cavities (ave. = 13.0 m; T-test, $p < .0001$).

Cline (1977) used a 5 class system to describe relative decay state: Class 1—a recently dead, hard snag with fine needles and branches remaining; Class 2—a hard snag with most of the bark remaining and fine branches gone; Class 3—early decay phase soft snag, with wood difficult to break by hand and bark sloughing; Class 4—advanced decay with bark blocky and wood easily hand broken; and Class 5—advanced decay with wood extremely soft and nearly humus.

Snags in Decay Class 1 were significantly selected against for cavity excavation in all forest management treatments ($p < .005$) and when compared to all snags ($p < .005$). Decay Class 2 was selected against when compared with total snags ($p < .05$). Snags in Decay Class 3 were significantly selected for cavity snags well above their availability on all treatments and when compared with total snags ($p < .005$). Class 4 snags were neutral in selection for total snags, but indicated selection on the dense shelterwood treatment *(table 5).*

Broken top snags were significantly selected as cavity snags on unmanaged plots and within the total snag population. On all managed plots, however, selection of broken top snags was not significant, likely because of the large proportion of snags existing on managed plots that were broken mid-stem.

Different tree species produce snags with different characteristics, affecting use for cavity excavation by PCE birds. Douglas-fir was the most consistently selected species of cavity snag; selection for this species was significant in the unmanaged treatment plots ($p < .005$) and for all available snags ($p < .005$). Ponderosa pine was selected for cavity excavation on the unmanaged plots (the only treatment where this species occurred) and for total snags. Western larch and lodgepole pine were selected against for cavity snags. Grand fir was neutral in selection when compared with total snag frequency. This suggests that grand fir is not preferred when other species are available, but is utilized when more preferred species are not present. Species selection for cavity snags was neutral in dense shelterwood and seed tree treatments *(table 6)*.

Table 4—*DBH of cavity and non-cavity snags with T-test results.*

Treatment and plot[1]	Cavity n	n	Cavity DBH (cm)	Non-cavity Mean DBH	P>[T]
Unmg					
Goo	56	354	53.3	24.9	.0001
SFk	53	388	51.9	21.7	.0001
NFk	45	235	40.0	19.3	.0001
Dshr					
Tan	19	188	33.1	19.6	.0015
Til	13	159	32.8	20.3	.0144
Seed					
Fro	29	49	57.4	24.3	.0000
Cur	24	26	50.2	31.8	.0011
Total snags	239	1,399	47.9	21.9	.0001

[1] Treatment: Unmg = Unmanaged, Dshr = Dense Shelterwood, Seed = Seed Tree
Plot names: Goo = Gooseberry, SFk = South Fork, NFk = North Fork, Tan = Taneum, Til = Tillman, Fro = Frosty, Cur = Currant

Table 5—*Decay class of cavity and non-cavity snags.*[1]

Treatment	Decay 1	Decay 2	Decay 3	Decay 4
Unmn[2]	x*	x	+*	0
DShltr	x*	0	+*	+
Seed	x*	0	+*	0
Total snags	x*	x*	+*	0

[1]Results from 2 category X^2 tests; @ p=.05, + = Selected for,
x = Selected against, 0 = no selection;
* = significant at <.005

[2] Unmn = Unmanaged, Dshltr = Dense Shelterwood

Table 6—*Tree species selection for cavity snags.*[1]

Treatment	ABGR[2]	LAOC	PICO	PIPO	PSME
Unmn[3]	x	x*	x*	+*	+*
DShltr	0	0	.	.	0
Seed	0	0	.	.	0
Total snags	0	x*	x*	+*	+*

[1] p=.05, + = Selected for, x = Selected against, 0 = no selection;
* = significant at <.005

[2] ABGR = Grand fir, LAOC = W. larch, PICO = lodgepole pine, PIPO = ponderos pine, PSME = Douglas-fir

[3] Unmn =Unmanaged , DShltr = Dense Shelterwood

Active PCE Nests

Active nest trees were significantly larger in diameter (n = 40, ave. = 56.9 cm) than cavity snags (n = 239, ave. = 47.9 cm; T-test, $p < .001$). Active nest trees were also significantly taller than cavity snags (active nest trees ave. = 13.8 m, cavity snags ave. = 9.8 m; T-test, $p < .05$). Nest trees used by Williamson's sapsuckers had the largest diameter (n = 4, ave. = 92.1 cm). Nest trees used by the two species with the largest number of observed nests, northern flicker and red-breasted nuthatch, had similar diameters at 53.4 (n = 14) and 56.8 cm (n = 13), respectively. Northern flickers used the shortest nest snags; they consistently were found nesting in broken off, well-rotted snags in the managed forest treatments. Broken tops were found on 73 percent of active nests and 83 percent of cavity snags.

Fifteen percent of active nests were in either live trees or Decay Class 1 snags. Twenty percent of active nests were in Decay Class 2, and no nests were found in Decay Class 4. Sixty-five percent of active nests were in Decay Class 3 snags, a category previously shown as selected for excavation.

Fifty percent of active nests were in Douglas-fir, a species also found to be significantly selected for cavity excavation. Thirty-five percent of active nests were in grand fir, a species not significantly selected in cavity snags. The active nests in grand fir were mostly northern flicker nests on the seed tree plots, where large diameter, broken-topped, Decay Class 3, grand fir snags were available and well used by flickers. Western larch nest sites were primarily those of Williamson's sapsuckers, in live trees. No nests were found in lodgepole pine, a species also not selected as cavity snags. Three nests were found in ponderosa pine, in areas with low abundance of this snag species. The hypothesis that ponderosa pine is a preferred cavity species is also supported by the significant selection for ponderosa pine for cavity snags Preferred characteristics of nest snags identified in this study were: large diameter (>50 cm), medium height (> 9 m), Decay Class 3, Douglas-fir, or ponderosa pine with a broken top.

Relative frequencies of tree species selected for cavity excavation were similar for those for known nest sites. Grand fir, Western larch, ponderosa pine and Douglas-fir comprised all observed nests, and similarly comprised all cavity snags. A slightly higher percent of observed nests were in Grand fir (32 percent) than for cavity snags (28 percent), and a slightly higher percent of cavity snags (57 percent) were in Douglas fir than for known nests (50 percent). Western larch had exactly the same percent of observed nests as cavity snags (10 percent).

PCE Densities and Species Composition

The highest PCE species transect counts during this study were, in descending order: red-breasted nuthatch, mountain and chestnut-backed chickadee, hairy woodpecker and northern flicker *(table 7).* Total PCE plot densities decreased from highest levels in unmanaged stands, to intermediate levels in dense shelterwoods, to lowest levels on seed tree plots. Species composition was also significantly different among management treatments *(table 8).* The species group identified for unmanaged plots, was dominated by small excavators: red-breasted nuthatch, mountain chickadee and chestnut-backed chickadee. Highest red-breasted nuthatch counts were found on the Gooseberry and South Fork plots, which were unmanaged stands with large trees and high snag densities. The species group found on unmanaged plots also included three-toed and black-backed woodpeckers, species known to be associated with fires, high snag densities, and recently killed trees (Bock 1974, Herr 1992).

The species compositions of birds found on unmanaged and seed tree plots were distinctive, while the species composition of birds on the dense shelterwood plots were an intermediate mix between the other two treatment types (Duncan's Multiple Range Test, *table 8)*. Hairy woodpeckers were counted most often on a dense shelterwood plot (Taneum), but occurred in all treatment types. Other species found on dense shelterwood plots included those found on unmanaged forest plots (red-breasted nuthatch, chickadees, pileated and hairy woodpeckers), and a small number of birds also found on the seed tree plots (red-naped and Williamson's sapsucker, and northern flicker). The PCE group found on seed tree plots included the largest proportion of a single species on any treatment, northern flicker. Red-naped and Williamson's sapsuckers were observed most often on seed tree plots, but were still uncommon.

Table 7—*Average density/15 ha by bird species by treatment.*[1]

Treatment	RBNU	TCH[2]	PIWO	HAWO	TTWO	BLWO	RNSA	WISA	NOFL	Total
Unmg[3]	9.87	6.00	.20	.94	.21	.43	0	0	.16	17.84
DShr	4.50	3.54	.20	1.10	0	.06	.06	.14	.34	9.97
Seed	.04	.30	0	.69	0	.08	.11	.50	4.04	5.77

[1] See *table 1* for bird species abbreviations.

[2] TCH= Total chickadees, mountain and chestnut-backed combined.

[3] Unmg = Unmanaged, DShr = Dense Shelterwood

Table 8—*Bird species composition shift summarized by treatment.*[1]

		Treatment	
PCE species	Unmanaged	Shelterwood	Seed tree
RBNU[2]	X	X	
TCH	X	X	*
PIWO	X	X	
HAWO	X	X	X
TTWO	X		
BLWO	X	*	*
RNSA	*	*	
WISA	*	X	
NOFL			X

[1] X = major component; * = minor component

[2] See *table 1* for bird species abbreviations.

PCE Bird Densities and Habitat Variables

Relationships of PCE bird densities by species with habitat variables were investigated using stepwise multiple regression analyses. A close correlation was found showing density of red-breasted nuthatches best predicted by snag densities in the 25-50 cm diameter class (R^2 = .94). Total chickadee densities were also best predicted by snag densities in the same diameter class (R^2 = .83). In both cases, greater densities of these small PCE birds were found in habitats with greater densities of snags. No habitat variables significantly predicted densities of hairy woodpeckers. Similarly, no significant relationships were distinguished for densities of pileated woodpecker, three-toed woodpecker, black-backed woodpecker or red-naped sapsucker, likely due to small sample sizes for these birds. Williamson's sapsucker and northern flicker densities varied significantly and inversely with canopy closure in regression analyses ($R^2 = .96$, and $R^2 = .91$, respectively). Total PCE bird abundance was best predicted by snag density >25 cm DBH ($R^2 = .93$).

Discussion

Snag Selection

Observed feeding snags, cavity snags and observed nests shared many characteristics. All were larger diameter and in advanced decay states, often with broken tops. Larger diameter snags may be needed to meet the thermal and mechanical needs dictated by the size of the PCE birds (Thomas and others 1979). Most excavated cavities and nests occurred in broken off snags, likely due to the increased opportunity for introduction of various stem rots, thus facilitating excavation. Many excavated cavities were observed within a few meters of the break off point on the tree stem. Because of the variability introduced by these broken tops, height is a poor measure of suitability of snags for PCE birds, other than to help determine acceptable minimums and target heights for snag viability in management. These results strongly suggest that larger snags may be critical to PCE birds.

Decay Class indicated time since death of the tree and affected characteristics important to PCE birds. Snags in Decay Class 1 were recently dead and probably had not been dead long enough to develop substantial insect populations or accumulated evidence of PCE feeding. Class 2 snags probably had active insect populations available for PCE birds. By the time a snag reached Class 3, enough time had elapsed for such activity and evidence to accumulate; hence, significant selection for this Decay Class was found. Snags in Class 4 were very decayed, often with large areas of missing bark, with evidence of PCE bird use obscured by the effects of decay. Decay class 3 snags showed the highest abundance of feeding evidence, but this was probably the result of accumulation over time, and does not demonstrate an immediate feeding preference for decay class. Because of the cumulative nature of feeding evidence on snags, analysis of feeding selection in decay class was inconclusive.

Snags in Decay Class 3 were significantly selected for cavity excavation on all plots, treatments, and for total snags. In addition, 65 percent of observed active nests were in Decay Class 3 snags. Snags in earlier Decay Classes were likely not softened enough by decay to facilitate excavation. Some excavation occurred in Class 2 snags (20 percent of nests), usually in portions of the stem with decay.

As expected, similar tree species were selected for cavity snags and observed nests, with Douglas-fir and ponderosa pine preferred. Western larch was selected for feeding snags but not for cavity snags. This may have been due to the smaller average diameter for most western larch present on the study sites, which may have been insufficient for cavity excavation. Lodgepole pine was not selected for any excavations, and this is consistent with the literature, implying that this species, may not be a good choice for retention if PCE birds are an objective. Grand fir was neutral for feeding selection, but was sometimes used for cavities. Grand fir wood appears to decay more quickly than other species, perhaps supplying a less durable substrate for nest cavities. Our data, however, suggest considerable PCE bird use of grand fir on the east side of the Cascades. The role of grand fir as a component of PCE habitat needs further investigation.

We found that snags are used by PCE birds for feeding in earlier decay states than those snags chosen for nesting. Habitat needs of PCE birds, therefore, encompass snags in all stages of decay. Additionally, because decay progresses through time, live and declining trees must be maintained after timber harvests as replacement snags. Results from this study support the work of many others in identifying snags in more advanced decay classes as particularly valuable habitat elements for PCE birds (Conner and others 1976, Madsen 1985, Raphael and White 1984). The need for snags with advanced decay means that snag management is a long-term endeavor, requiring protection of existing snags and an adequate supply of all diameter “legacy” snag recruits to be maintained over time.

The significant selection by PCE birds for broken tops may be explained by a preference for snags with more decay, and perhaps increased insect activity. Broken top snags probably collect precipitation moisture directly into their stems, thus improving fungal growth conditions and allowing the broader introduction of wood-softening fungi.

Active nests were found in significantly larger stems than cavity snags, lending support to the conclusion that PCE birds prefer large snags for nest cavity sites. Known nest snags were also found to be significantly taller than cavity snags in this study. The minimum height of an observed nest tree in this study was 2.1 m, which is similar to the minimum height of snags (2 m) recommended by Thomas and others (1979). This minimum, however, constitutes a poor management guideline. The influence of decay, rather than height, is likely the most important factor regarding cavity site location by PCE birds. Height is only relevant as a management (i.e., safety) factor.

The active nest sample effectively acted as a control group to compare with measured cavity snags, adding considerable meaning to the data set. The most numerous observed nests were those of red-breasted nuthatches and northern flickers. Nuthatch nests were found predominantly in large diameter, highly rotted stems in unmanaged stands with high densities of large trees and snags. Flicker nests were located exclusively in seed tree areas, where large DBH, short stubs (residuals from the mature, pre-logged stand) were likely retained because they posed no safety hazard to logging operations. Northern flicker nests were found mostly in large-diameter, broken-top, well-decayed grand fir snags. These two species were the most different in habitats used in this study, yet their nest snag characteristics were very similar. This suggests that the characteristics of snags preferred by PCE birds are consistent across habitat types.

PCE Bird Density and Abundance

Red-breasted nuthatch densities were most closely predicted in the regression analyses by density of snags between 25 and 50 cm DBH (R^2 = .94). Habitat with high densities of snags of this diameter category was most prevalent in unmanaged forest. Basal area was the second predictor for red-breasted nuthatch density in our study, suggesting a preference for denser forests. These plots also had the highest abundance of large diameter trees. Other researchers have found that red-breasted Nuthatches prefer older forest stands with larger stems and high structural diversity (Adams and Morrison 1993, Mannan and Meslow 1984). Timber harvest, which simplifies stand structure, opens the canopy, and removes large stems and dead wood, undoubtedly reduces habitat quality for red-breasted nuthatches.

Chickadees nest and feed in dead, rotting wood, and utilize thick forest and brushy areas in northwestern coniferous forests (Thomas and others 1979). Our study reinforced this finding, as we documented decreased abundance of chickadees in dense shelterwood plots, compared to unmanaged forest, and lowest abundance in seed tree plots. Chickadees are also likely to be negatively impacted by timber harvest in the central Cascades, which reduces forest complexity and snag density.

Black-backed and three-toed woodpeckers were observed in highest densities on the North Fork and South Fork plots, areas with high densities of relatively small snags *(tables 3, 8).* The literature also reports that these woodpeckers nest in smaller snags than many other PCE birds (McClelland and others 1979, Thomas and others 1979). The four nests occupied by these species in this study were in smaller snags (diameter range 26.7 to 34.4 cm dbh, n = 4), suggesting that these two species may be able to utilize younger stands.

Pileated woodpeckers were counted on all unmanaged plots and on both shelterwood plots, but in low densities *(table 8).* These birds are known to have large territories, estimated between 200 and 689 ha (494 to 1,650 acres) for similar habitat types in the Blue Mountains of Oregon (Bull and Holthausen 1993). These woodpeckers were not tallied on the seed tree plots where canopy closure, tree density, and snag density were all relatively low. Heavy timber harvest probably negatively effects this species, but their presence on the dense shelterwood plots in our study suggests that active forest management that retains adequate dead wood for feeding, nesting, and roosting needs, may result in habitat that remains suitable for pileated woodpeckers.

Williamson’s and red-naped sapsuckers were found more frequently on the more open plots in our study, perhaps as a reflection of increased visibility, rather than higher densities. Previous work (Madsen 1985, Raphael and White 1984) found Williamson’s sapsucker nest sites to occur largely in areas of dense snags and high basal area. Our result may suggest that sapsucker breeding territories are determined by the presence of adequate suitable structures, such as large diameter western larch, rather than forest density.

Northern flickers prefer habitats where open ground for feeding and snags for nest sites occur together (Ehrlich and others 1988). Flicker densities were most closely predicted by canopy closure in this study (R^2= .82), showing a distinct preference for open, meadow-edge habitat types, represented in this study by seed tree plots. Their breeding presence, however, is probably limited by the availability of suitable snags. Seed tree plots with snags present may represent nearly optimal habitat for breeding northern flickers, based upon their density as the third highest for any species by treatment in this study *(table 7).* Western bluebirds and Kestrels commonly utilized old cavities, most likely excavated by flickers, on the seed tree plots.

Methods

The bird count method utilized in this study may have resulted in undercounts of birds in the unmanaged and dense shelterwood habitats due to the quiet nature of woodpeckers during the latter portion of the breeding season when many of our transects were measured. In addition, observer bias in distance estimation can be a significant problem that affects results in bird surveys that we employed. In future PCE studies or monitoring, we recommend using simple transect or point counts, thus minimizing distance estimates. We also recommend use of as few highly trained observers as possible conducting all surveys, to eliminate intra-observer bias. Two different field assistants in 2 years complicated results on this study, particularly in reference to chickadee identification. PCE bird monitoring and research should include red-breasted nuthatches. We observed these birds excavating cavities in soft wood, and their calls are quite distinctive. If possible, surveys should occur earlier in the breeding season, beginning in April and ending in early June. This would more closely coincide with territorial displays. Nest searches should occur in June and early July, when young are readying to fledge, and nests are easiest to find.

Treatment Effects

Treatments were not always uniform, and therefore effects were not entirely clearly evident. Approximately the same PCE bird species composition was found in the dense shelterwood plots as the unmanaged plots, but PCE birds were less abundant in the dense shelterwoods *(table 7).* While the life requirements of the PCE species were apparently met in the shelterwoods, some habitat limitation resulted in lower population density. It is possible that these shelterwoods are population sinks. It is noteworthy that the North Fork plot, although characterized as unmanaged forest, had snag densities more similar to the dense shelterwoods than the other unmanaged plots *(table 3).* PCE species composition and abundance measured on the North Fork plot were also more similar to those recorded on the dense shelterwood plots. These data support the hypothesis that snag abundance is likely a key habitat component supporting PCE density. Hairy woodpecker occurrence in all treatment types supports their description by several authors as habitat generalists (Mannan and Meslow 1984, Thomas and others 1979). The seed tree treatments held low numbers of all PCE bird species, except for northern flickers, suggesting that these highly managed areas were currently unsuitable habitat for most forest PCE species.

PCE Populations and Habitat

A strong relationship found in the regression analysis was between total birds and snag density > 25 cm ($R^2 = .94$). Therefore, density of large snags may be the most important habitat component affecting PCE bird abundance in grand fir forests in eastern Washington. Our study supports conclusions of similar research (Raphael and White 1984, Zarnowitz and Manuwal 1985). The maintenance of adequate densities of larger snags, with a continuum of decay conditions present at all times, is undoubtedly a significant factor in sustaining populations of PCE birds.

Preferred Snag Characteristics and Management Recommendations

Preferred species for PCE feeding snags are western larch and Douglas-fir and preferred species for cavity snags are Douglas-fir and ponderosa pine. Grand fir is also utilized, but may not be a preferred species. Snags should be maintained in all Decay Classes, particularly in Classes 2 and 3. Snags and green recruitment trees should be retained in the larger diameter classes (minimum of >35 cm (14 in) DBH) to provide a continuous supply of snags over time. This DBH is based upon the minimum nest snag utilized by hairy woodpeckers and northern flickers on this study. Minimum snag height should be 5 m (15 ft), based upon the observed minimum height of snag used by hairy woodpeckers. This is recommended as a management guideline rather than the minimum diameters and heights (25 cm and 2 m) determined by chickadees and used by many land management agencies. We maintain that snags should be managed for larger diameters and heights than currently practiced to provide the best chance of population viability for the host of cavity dependent species. Large diameter western larch should be retained in forest management because of the importance of these trees for Williamson’s sapsuckers.

Maintaining high snag densities alone will not provide quality habitat for PCE birds. Snags with specific characteristics (Decay Class, broken tops, and species) must also be maintained. The importance of decay trajectories to habitat use by PCE species remains a rich area for future research. In addition, target bird species compositions and territory sizes should be considered in PCE management.

Despite the well-documented fact that snags are important components of forest ecosystems, they are often removed from forest stands during timber harvest, forest management activities, and for fuel wood. Cutting of the largest snags (especially Douglas-fir and Western larch) for firewood is a common practice throughout the Northwest, but contributes to habitat degradation for all cavity species. Snags are also cut for hazard reduction at parks and public facilities. Quality wildlife trees are often removed during logging that could have been maintained through planning and forethought. Protection of existing high quality snags and maintenance of adequate recruitment trees must become more widely recognized as key tools for forest biodiversity preservation, and elevated to common practice. This would promote healthy populations of cavity nesting birds and associated species across the forested landscape over time.

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Cavity-nesting Bird Use of Snags in Eastside Pine Forests of Northeastern California[1]

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Abstract

Relationships between snags (standing dead trees) and cavity-nesting birds were examined in the breeding seasons of 1989, 1990, 1991 on the Modoc and Lassen National Forests and Lassen Volcanic National Park, California. Transects, that differed by snag density, were randomly placed in eastside pine habitat patches dominated by either ponderosa *(Pinus ponderosa)* or Jeffrey pine *(P. jeffreyi).* Snags with active nests had greater diameters and were taller than random alternative snags; both differences were significant ($P > 0.05$). Snags with historical nest cavities generally were of larger diameter than snags without historical nest cavities. Despite the heavier nesting use of larger snags, many large snags, with similar visual deterioration characteristics, showed no indication of historical nesting use.

Introduction

Snags (standing dead trees) are an important component of forests and play a crucial role in the continuation of soil fertility as well as perpetuation of species that depend on snags for parts of their life histories (e.g., snag associated insects, substrates for vertebrate nesting, and roosting cavities) (Bull and others 1997, Machmer and Steeger 1995, Parks and others 1997). Some bird species, because of their need for cavities in which to nest (i.e., natural cavities, existing excavated cavities, or suitable conditions for the excavation of new cavities), find suitable nesting substrate in snags or live trees with patches of decay or cavities resulting from limb breakage. Some 85 species of North American birds, not to mention numerous other vertebrates and invertebrates, construct nests in snags, or nest in natural cavities, or previously excavated holes in snags (Scott and others 1977). Availability of nest sites may limit the numbers of cavity-nesting species.

Snag size, especially diameter, and to a lesser extent height, are also thought to be important characteristics related to bird usage. Generally, larger diameter snags are used in preference to smaller diameter snags (Bull 1975, Cunningham and others 1980, Mannan and others 1980, McClelland and Frissell 1975, Milne and Hejl 1989, Raphael and White 1984, Scott 1978, Scott and Oldemeyer 1983). To the contrary, Hay and Guntert (1983) concluded that smaller snags are preferred by some species

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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for purposes other than nesting. Many authors consider the presence of snags to be essential for the continued presence of cavity-nesting birds.

The eastside pine forest of California is characterized by relatively open stands of pine with relatively few snags compared to other western forests. Preliminary surveys of this forest in 1988 indicated that very large portions of the Modoc and Lassen National Forests had well under one snag to the acre. The paucity of snags is related to the lower tree densities inherent in these stands as well as past management activities. In the late 1980s, the USDA Forest Service became concerned about the effects of this perceived current and future snag deficit on cavity-nesting birds.

To gain a better understanding of the effects of snag densities on cavity-nesting birds, a study was designed to examine the relations between snag numbers and numbers of cavity-nesting birds. The study also collected information on the characteristics of snags used by these nesting birds. This paper contrasts the characteristics of snags used by actively nesting birds with the characteristics of snags available in close proximity but not used; and it will contrast the characteristics of snags used currently with those used by nesting birds in the past.

Methods

Study Areas

The 24 study areas are located in eastside pine forests of Modoc, Lassen, and Shasta Counties, California. These forests are dominated by ponderosa pine *(Pinus ponderosa),* Jeffrey pine *(P. jeffreyi)* in some locations, and white fir *(Abies concolor)* with smaller amounts of incense cedar *(Calocedrus decurrens),* western juniper *(Juniperus occidentalis),* California black oak *(Quercus kelloggii),* and lodgepole pine *(P. contorta).* Dominant shrubs include big sagebrush *(Artemisia tridentata),* bitterbrush *(Purshia tridentata),* and mahala mat *(Ceanothus prostratus);* with lesser amounts of Nevada manzanita *(Arctostaphylos nevadensis),* curl-leaf mountain-mahogany *(Cercocarpus ledifolius),* and silver sagebrush *(Artemisia cana).*

Study Design

Snag densities were estimated for approximately 1,000 land management polygons on the Modoc and Lassen National Forests, and suitable areas within Lassen Volcanic National Park. Study areas were randomly selected from the pool of potential study areas in seven snag density classes: 0, >0 to ≤0.20, >0.20 to 0.40, >0.40 to ≤0.61, >0.61 to ≤0.81, >0.81 to ≤1.21, and >1.21/hectare. All of the lesser snag density classes had sufficient numbers of potential study areas from which to randomly draw the study areas. For the two densest snag density classes, all areas found with such densities were used in the study. One 100 x 500 m long strip transect was placed randomly within each of the 24 selected study areas; the bounds of these areas were used as the basis of all subsequent work.

Active Nests

From 1989 through 1991, each transect was searched for nests, especially of cavity-nesting birds. Nests were located by following birds back to their nests, visually examining potential nest holes for indication of recent excavation, and watching and listening for nesting activity (e.g., carrying nesting material, food delivery, hearing the sounds of young birds).

At active nests, information was collected on tree or snag species, diameter at breast height (DBH), total height, nest height, nest hole diameter, compass direction the nest hole faces, and whether the nest was constructed in living or dead portions of the tree. For each active nest tree, the nearest random alternative snag or live tree, without an active nest, was also identified. Information collected from this snag or tree was species, DBH, height. If either the nest snag or alternative site was a snag included in the snag inventory, the snag number was also recorded linking the nest or alternative site to the snag characteristics data collected under snags.

Historic Nest Holes

All snags with diameters in excess of 15 cm were permanently marked, mapped, and information including species, diameter, height, percent bark remaining, and number of nest holes were taken on 23 of the 24 study plots in 1989. On one plot, the number of small snags (<25 cm in diameter) was so great that information was taken only on those snags with diameters in excess of 25 cm.

Analysis

Primary and secondary cavity-nesting bird species found nesting in the study areas were red-breasted sapsucker *(Sphyrapicus ruber),* Williamson's sapsucker *(Sphyrapicus thyroideus),* hairy woodpecker *(Picoides villosus),* white-headed woodpecker *(Picoides albolarvatus),* black-backed woodpecker *(Picoides arcticus),* northern flicker *(Colaptes auratus),* pileated woodpecker *(Dryocopus pileatus),* tree swallow *(Tachycineta bicolor),* mountain chickadee *(Poecile gamblei),* red-breasted nuthatch *(Sitta canadensis),* white-breasted nuthatch *(*Sitta carolinensis), pygmy nuthatch *(Sitta pygmaea),* brown creeper *(Certhia americana),* house wren *(Troglodytes aedon),* and mountain bluebird *(Sialia currucoides)*.

Comparisons of individual species were based on the four with the greatest number of nests found: hairy woodpecker, mountain chickadee, red-breasted nuthatch, and pygmy nuthatch. Characteristics of snags with active nests were compared to alternative nest snags using t-tests and box plots. Information on historical nest holes and nesting snags (of snags >15 inches in DBH) was taken from data collected in 1990.

Results

Active Nests

Over the 3-year bird study period, 110 active nests of cavity-nesting birds were located. All but four of these nests were in ponderosa or Jeffrey pines. The majority of nests were of hairy woodpecker (17), mountain chickadee (12), red-breasted nuthatch (11), and pygmy nuthatch (16).

On occasion, live trees were used for nesting and most of the cavity-nesting bird species took advantage of such sites. Eight nests (7 percent of total) were found in live trees; these sites include the dead tops of large diameter pine trees, a crack in the bole of a large tree, other damaged areas where the bark was lost, and a dead limb in a western juniper. Half of the live tree nests were on transects with more than 0.4 snags greater than 38 cm in diameter during the bird study time period (see Landram and others 2002 for a discussion of snag demography on these study areas).

Mean DBH of snags used for nesting were in excess of 70 cm for the four birds of interest *(fig. 1)*. The smallest diameter used by all four species was approximately 40 cm. Although the smallest diameters used by each species approximated 40 cm, the largest diameters were quite variable ranging from <100 (mountain chickadee) to approximately 180 cm (red-breasted nuthatch).

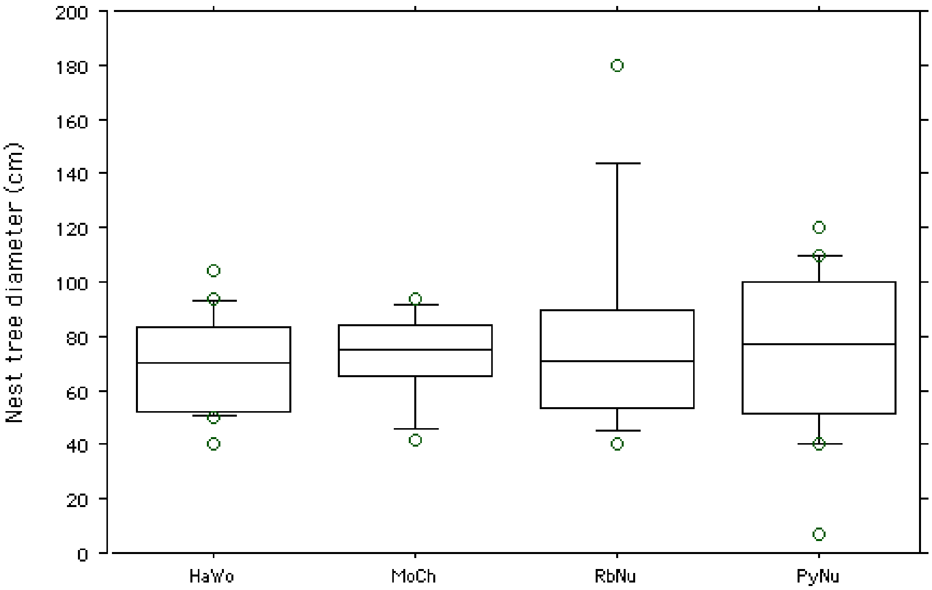

Figure 1—Mean diameters (cm) of nesting snags used by hairy woodpecker (HaWo - n = 17), mountain chickadee (MoCh - n =10), red-breasted nuthatch (RbNu - n = 11), and pygmy nuthatch (PyNu - n = 16) ± 1 standard error and values for the largest and smallest nest tree diameter.

Heights of snags used for nesting ranged from less than 5 m (mountain chickadee) to more than 45 m (red-breasted nuthatch) *(fig. 2)*. The shortest trees used by each species was between 7 and 9 m in height except for mountain chickadee—one nest at 3 m and two at essentially 0 m (both in downed logs). Tallest trees used approached the maximum available. Despite this variation in the ranges in nest tree height by species, mean heights of nest trees selected by each species were not very different with the exception of hairy woodpecker, which generally used shorter trees than the other three species.

Nest heights were quite variable: hairy woodpecker nests generally were higher than the other three species, and mountain chickadee nests generally were lower than the other three species *(fig. 3)*. Range of nest heights was from about 2 m for all except mountain chickadee to 20 m and above. Several mountain chickadee nests were in logs nearly at ground level.

Trees selected for nesting differed significantly in diameter *(fig. 4)* (t-value = 6.774; df = 106; P-value <0.0001) and height *(fig. 5)* (t-value = 2.916; df = 106; P-value = 0.0043) from the nearest randomly selected trees.

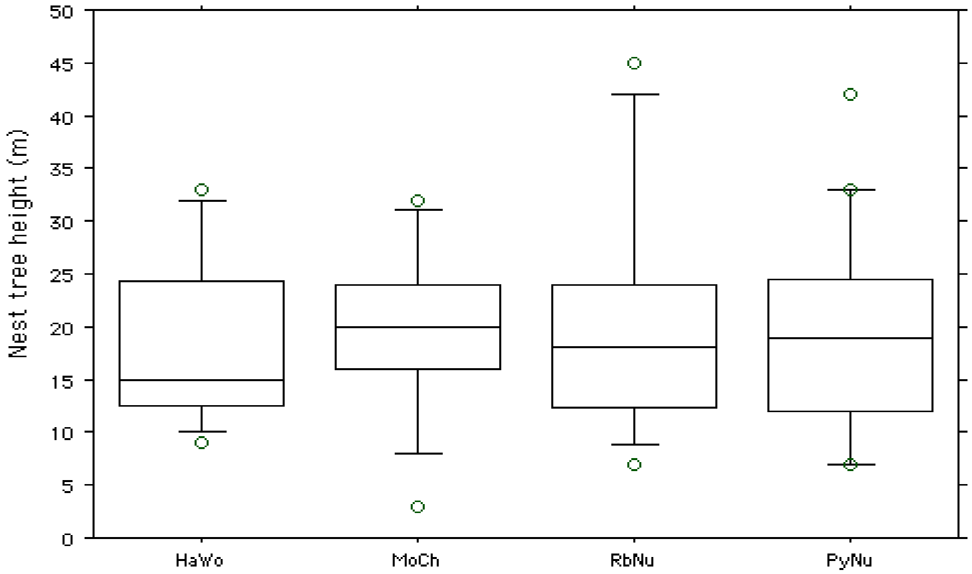

Figure 2—Mean heights (m) of nesting snags used by hairy woodpecker (HaWo - n = 17), mountain chickadee (MoCh - n =10), red-breasted nuthatch (RbNu - n = 11), and pygmy nuthatch (PyNu - n = 16) ± 1 standard error and values for the tallest and shortest nest trees.

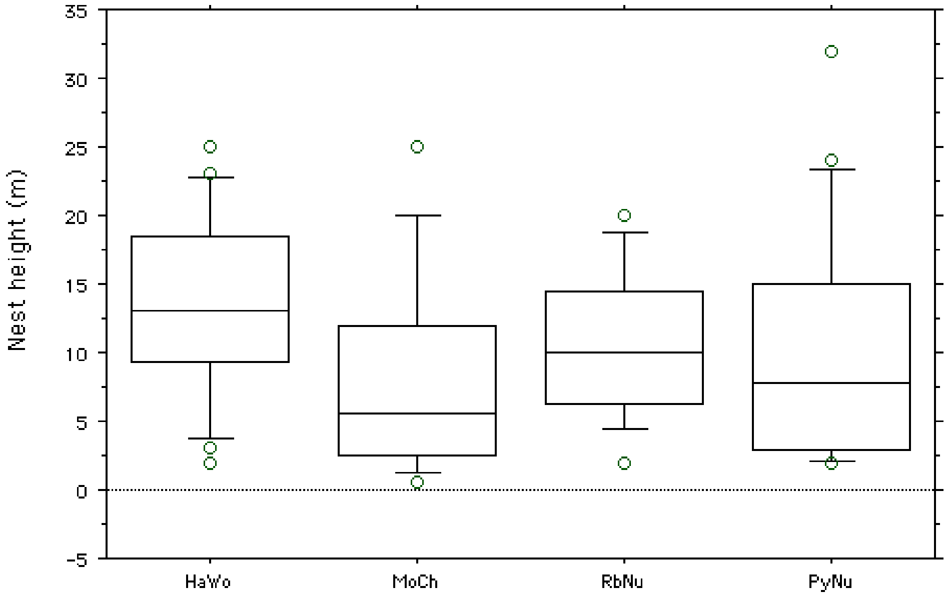

Figure 3—Mean nest heights (m) of hairy woodpecker (HaWo - n = 17), mountain chickadee (MoCh - n =10), red-breasted nuthatch (RbNu - n = 11), and pygmy nuthatch (PyNu - n = 16) ± 1 standard error and values for the highest and lowest nest locations.

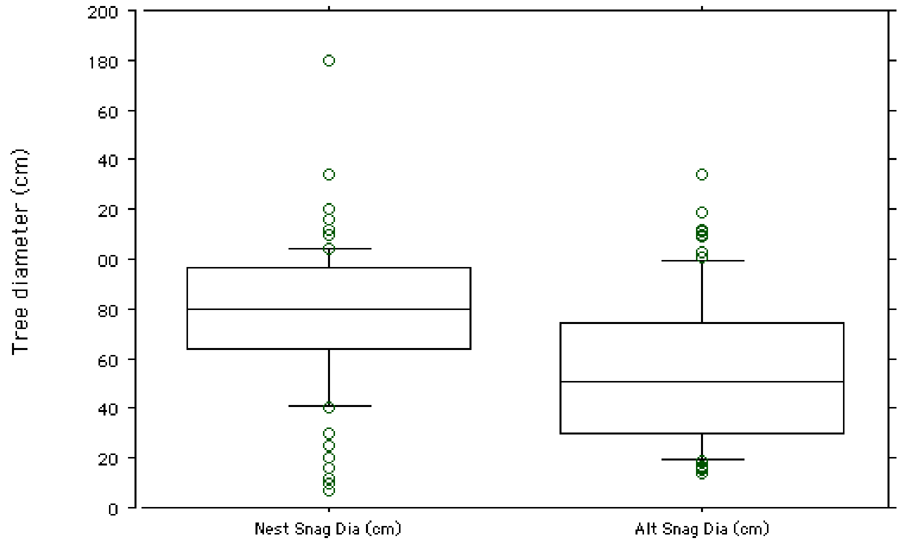

Figure 4—Comparison of nest snag diameters (cm) to diameters of alternative snags (n = 107). The box plots display the 10th, 25th, 50th, 75th and 90th percentiles of each variable.

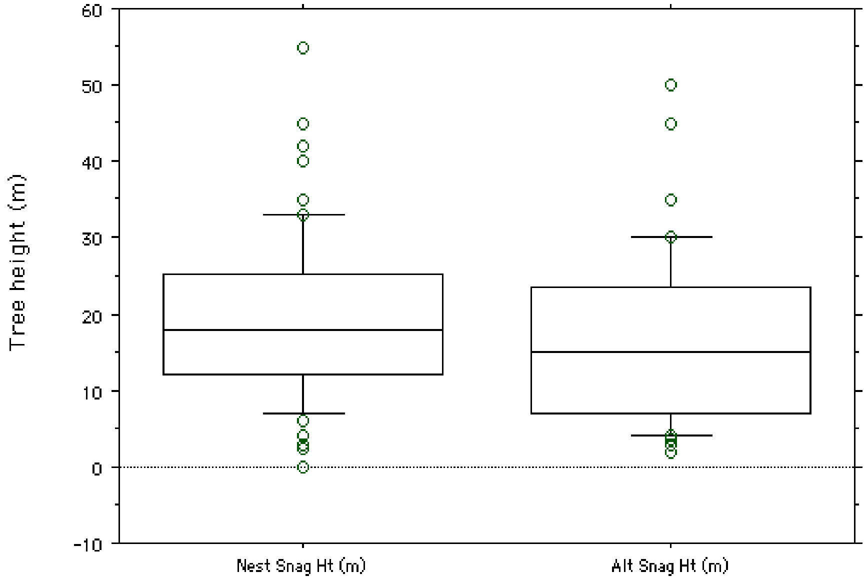

Figure 5—Comparison of nest snag heights (m) to heights of alternative snags (n = 107). The box plots display the 10th, 25th, 50th, 75th and 90th percentiles of each variable.

Historic Nest Holes

In 1989, a total of 1,459 snags of 9 snag species were found on the 24-5 ha study plots *(table 1)*. Nest holes were not found in any of the California black oak, incense cedar, lodgepole pine, red fir, or western juniper snags on any study plot. Of the tree species with nest holes, Jeffrey pine, ponderosa pine, and white fir, only about 15 percent of the snags of each species had at least one nest hole *(fig. 6)*. For the fourth category, unknown pine (Jeffrey or ponderosa pine but too deteriorated to determine which species), some 35 percent of the snags had at least one nest hole. Snags with more than eight nest holes were very rare and found only in Jeffrey and ponderosa pines.

For the four taxa of snags with nest holes, as snag diameter increased, generally a higher proportion of snags had nest holes *(fig. 7)*. Almost none of the snags in the 0-30 cm diameter class had nest holes regardless of species but between 10 (white fir) and 100 percent (unknown pine) of the >120 cm diameter class had nest holes.

Numbers of nest holes relative to the numbers of snags increase as diameter class increases *(fig. 8)*. Except for white fir, snags in larger diameter classes generally had greater numbers of nest holes than did snags in smaller diameter classes.

Table 1—*Numbers of snags present by snag species across all 24-5 ha study plots in 1989.*

Snag species	No. of snags
California black oak	4
Incense cedar	27
Jeffrey pine	843
Lodgepole pine	30
Unknown pine	35
Ponderosa pine	269
Red fir	1
Western juniper	66
White fir	184
Total	1,459

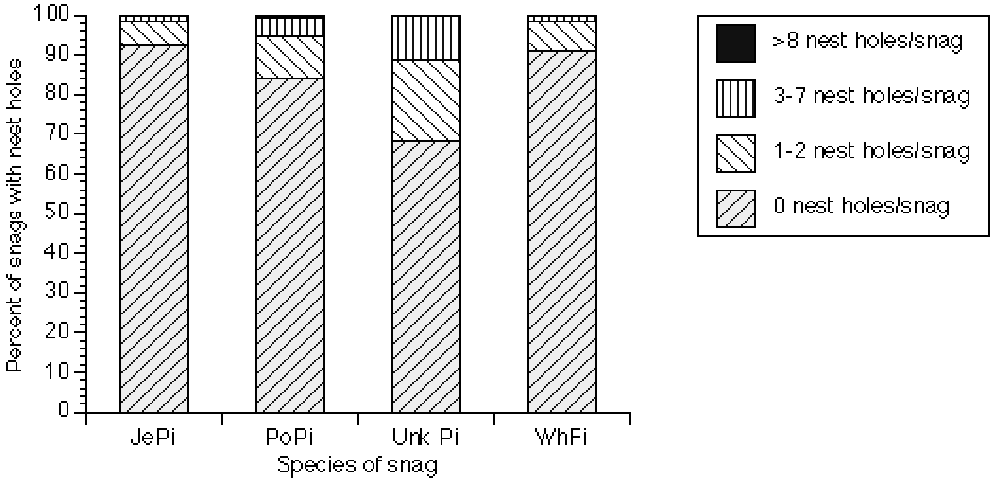

Figure 6—Percentages of snags with historic nest holes, for the snag species that possessed more than one nest hole, ranging from 0 nest holes to more than 8. Jeffrey pine = JePi (n = 843), ponderosa pine = PoPi (n = 269), unknown pine = Unk Pi (n = 35), white fir = WhFi (n = 183). Both JePi and PoPi have snags with >8 nest holes per snag, but the percentages are too low (0.1 and 0.7 percent respectively) to be illustrated in the figure.

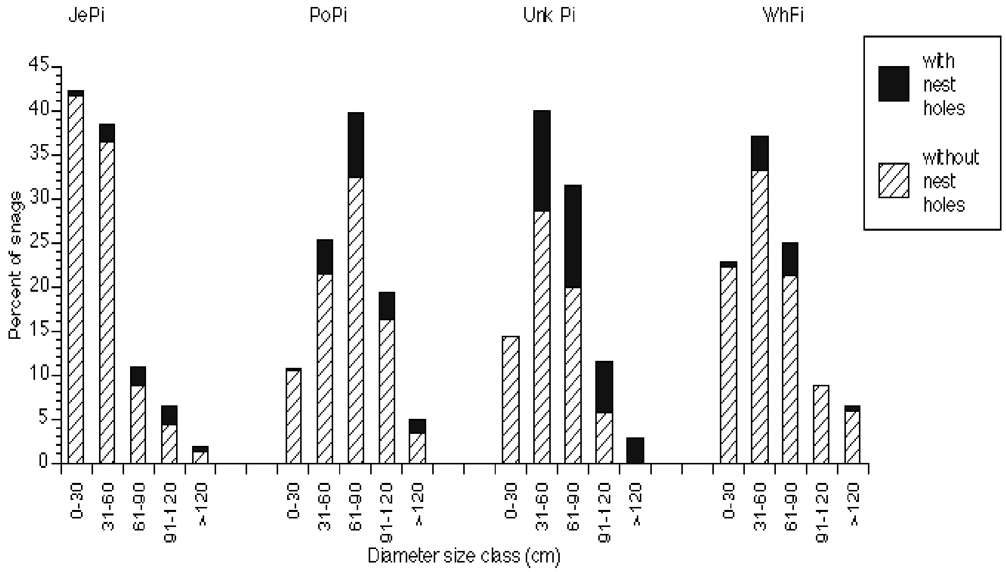

Figure 7—Percentages of snags by diameter class with historic nest holes, for the snag species with more than one nest hole, that had nest holes compared to those without any nest holes. Jeffrey pine = JePi (n = 843), ponderosa pine = PoPi (n = 269), unknown pine = Unk Pi (n = 35), white fir = WhFi (n = 183).

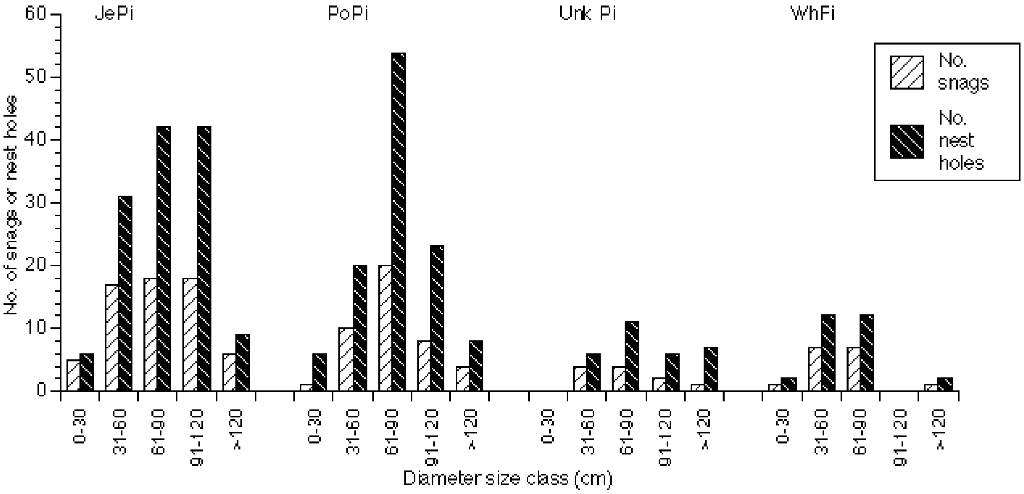

Figure 8—Numbers of snags by diameter classes with nest holes, for the snag species with more than one nest hole, compared to the number of nest holes in each diameter class. Jeffrey pine = JePi (n = 843), ponderosa pine = PoPi (n = 269), unknown pine = Unk Pi (n = 35), white fir = WhFi (n = 183).

Discussion

Active Nests

All four bird species nested in trees, generally dead or in the dead sections of live trees, that were greater than 40 cm DBH and with heights of nest trees that generally exceeded 10 m. The smallest diameter trees used approximate the lower limits of snag diameters found in many snag guidelines (e.g., Studinski and Ross 1986). The majority of the nests were in trees substantially larger in diameter than 40 cm DBH. Hairy woodpeckers often used shorter trees than the other species, but the majority of nests of all species were in trees in excess of 20 m in height. The heights of the nests, somewhat dependent on the height of the trees, was perhaps more variable than either the diameters or heights of trees selected for nesting. Hairy woodpeckers, despite selecting shorter trees on the average, tended to place their nests higher in the trees than the other species.

The assemblage of cavity-nesting birds generally placed their nests in trees larger in diameter and taller than randomly selected alternative trees found in the study areas. The difference in diameters was greater than the difference in heights, suggesting that tree diameter may be the more important variable driving nest tree selection. Another explanation is that tree diameters are more stable than tree heights, as tree height often becomes shorter as trees decay, whereas once the bark is lost tree diameters do not change measurably.

The selection of larger trees for nesting by cavity-nesting birds in California eastside pine forests reflects what is known from other forests and is well documented in the literature (e.g., Bull 1978, Cunningham and others 1980, Gutzwiller and Anderson 1986, Gutzwiller and Anderson 1987, Mannan and others 1980, Mannan and Meslow 1984, McClelland and Frissell 1975, Raphael and White 1984, Rosenberg and others 1988, Swallow and others 1988). Larger trees are generally preferred over smaller trees for most cavity-nesting species.

Ponderosa and Jeffrey pines are the tree taxa most used for nesting in this study. These eastside pine forests are dominated by ponderosa or Jeffrey pine with other species of trees relatively uncommon. The pines were generally of larger diameter than the other tree species.

Sapwood decay in ponderosa pine, and perhaps Jeffrey pine also, tends to be rapid and the decayed sapwood is easily excavated in cavity construction (Parks and others 1997). Thus, the entire cross-section of potential nest trees may not be suitable for excavation, and trees larger in diameter than the nominal guidelines suggest may be necessary for nesting birds. For the larger-bodied species, larger diameter trees may even be more desirable.

Historic Nest Holes

When the study was initiated, nearly 1,500 snags were available for nesting. The numbers of snags per plot varied considerably from 0 on several plots to as many as several hundred in a few cases. The vast majority of snags did not contain any nest holes, and only a very few snags had more than two-nest holes. Some 10-15 percent of the ponderosa and Jeffrey pine and white fir snags had nest holes; and 25 percent of the unknown pine species snags had nest holes. Although many ponderosa and Jeffrey pine and white fir snags had not decayed to a state that would permit excavation of nest holes (i.e., obvious separation of the bark from the bole or loss of large portions of the bark, absence of needles and branchlets), the majority of unknown pine species snags had aged to a point where one might expect the birds to be able to excavate a nesting cavity. These pine snags had decayed to a state where they could no longer be classified into either ponderosa or Jeffrey pine using our field methods. However, even in these rather well decayed trees, a large number of snags did not have any nest holes. This suggests that a rather large number of the snags in this study were not suitable or capable for excavation of nest holes or that birds select snags for locating nest holes on criteria not readily apparent from the visual characteristics of the snags.

Zack and others (2002) reported that the majority of snags at Blacks Mountain Experimental Forest and Goosenest Adaptive Management Area did not have any cavities. However, more snags at Blacks Mountain had cavities than at Goosenest. Welsh and Capen (1992) also noted that relatively large numbers of apparently suitable nest trees were not used as nesting sites and also found that the number of excavated cavities per cavity trees were relatively low. Experimental evidence related to this question is not conclusive. Differences in habitat characteristics may influence the findings from snag and cavity studies. Waters and others (1990) reported that nest sites are not limiting to the secondary cavity-nesting bird community in an oak-pine woodland. However, Brawn and Balda (1988) showed that nest sites can be limiting for secondary cavity nesters in a ponderosa pine forest.

Birds apparently do not randomly choose snags in which to excavate a nest. The larger the diameter of the snag, the more probable it is to have had nest holes excavated in it. This is particularly apparent in ponderosa and Jeffrey pine, and unknown pine snags and, as indicated earlier, may be related to the portions of the trees where the decay takes place.

Management Implications

Snags with large diameters and heights (e.g., greater than 25 inches in diameter) have been identified as very important to many of the cavity-nesting bird species. Such snags can only be derived from large trees that have been given the time to grow large. Because of the commercial value of large trees, they appear to be in short supply across large landscapes in eastside pine forests. To best provide habitat for these cavity-nesting species, larger parcels of land should be managed to provide trees of a variety of sizes and permit some of the largest trees to become snags.

Management guidelines for specific snag densities are difficult to propose because the capability of the land to produce snags, especially large ones, is so variable, the snag resource is highly dynamic both in space and time, and many snags do not appear to be used as nesting substrate, suggesting that some snags may be surplus (as far as bird nesting is concerned). Balda (1975), as well as many others since, has proposed methods for estimating how many snags are needed by specific bird species. Application of those methods could form a baseline for specifying snag densities. However, snag numbers are probably related to the capability of particular sites to produce and sustain snags through time and related to site-specific variables, such as the number of large trees existing per acre, the lifespans of the large trees, and the mean standing duration of large snags. Snag numbers are also related to the historical consequences and causes of mortality (e.g., fire, insect attack) and their effects on the residual of large live trees that will eventually become snags. Thus, regardless of guidelines proposed, they will need to be tailored to specific landscape capabilities and conditions at the project scale.

Snags are dynamic “entities” on dynamic landscapes that emerge and fall at different rates, depending on a variety of conditions related to cause of mortality and site characteristics. As such, land managers cannot be expected to understand or manage the decay trajectories of each snag. Despite the uncertainties involved in snag management, snag condition, hardness or softness, or simply the age of the snag may be useful criteria for choosing snags for removal or retention. Generally, it seems that the longer a snag stands, the more opportunity it has to be used to excavate a cavity or provide an existing cavity for a secondary cavity nester to use. Old snags are usually not commercially valuable, and land managers should attempt to retain those that do not pose a substantial safety or fire risk. Specific snag objectives might then be based on retention of hard snags.

The removal of hazard trees and reduction of fuels can also reduce snag numbers substantially, especially in well roaded areas like northeastern California. It is often necessary to reduce hazards and reduce fuels, but removal of entire snags in many cases is not justified. Topping trees rather than total removal is an option that will maintain some, perhaps the majority, of the snag value yet reduce the hazards inherent in standing snags. Snag topping, as done on the Modoc National Forest (sawing off the tops; Studinski, pers. comm.) and at Yosemite National Park (pulling out the tops; Mattos, pers. comm.), may also permit snags to persist for a longer time. However, it is not yet known if such methods extend snag life, and it is not known how cavity-nesting species respond to such treated snags.

If there are fewer snags on landscapes of interest than desired, snags can be created by a variety of methods (see Shea and others 2002 for a discussion on snag creation methods and results). Depending on the agent used to create snags, such trees can provide habitat for cavity-nesting birds as well as other organisms. Even retaining stumps, cut as high as possible, will still retain some of the snag values for cavity-nesting birds. However, Morrison and others (1983) recommend that high-cut stumps be employed only when absolutely necessary for safety considerations.

Information about the relationships of cavity-nesting birds with snag characteristics can be used to craft management approaches to the conservation of the snag resource and cavity-nesting birds. However, managers must not predicate their management strategies only on providing nesting substrates. These birds require a continual sequencing of snags into their habitats for foraging as well as for nesting. In addition, cavity-nesting birds are not the only organisms that prefer or perhaps require dying and dead trees for their survival; a myriad of other organisms, including fungi, invertebrates, and other vertebrates, are also associated with these trees. Simply managing for the birds’ needs may not fulfill the requirements of other species that may actually be more essential to the processes in the forest, such as the recycling of wood.

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Woodpecker Foraging and the Successional Decay of Ponderosa Pine[1]

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Abstract

In 1998 we initiated a long-term study investigating the relationships between woodpecker foraging and snag decay processes in interior ponderosa pine forest communities located in Oregon and California. We describe temporal changes in snag structure and quantify both woodpecker foraging activity and relative sapwood decay in 144 ponderosa pine snags, ranging in age from 1 to 9 years (time since death). Preliminary results indicate that temporal changes in snag characteristics were reflective of both inherent insect activity and woodpecker foraging quality. Statistical analysis revealed no significant difference in cumulative woodpecker foraging abundance as snags aged, indicating that woodpecker foraging activity occurred primarily in the younger aged snags. Additionally, there was no correlation between woodpecker foraging intensity and relative sapwood decay. These results offer insights into the interactive biology of bark beetles, woodpeckers, and fungi in the decomposition of ponderosa pine.

Introduction

Woodpecker foraging and nesting ecology is closely tied to insect infestations and tree decomposition stages. Foraging woodpeckers tend to select trees and snags containing high levels of bark and wood boring insects (Baldwin 1960, Kroll and Fleet 1979, Otvos 1965), whereas nesting woodpeckers generally require pockets of older, decayed wood that permit nest excavation (Bull 1983, Bull and others 1997, Conner and others 1976, Harris 1983). In fact, Conner and others (1976) and Miller and Miller (1980) suggested that some form of wood decay is a prerequisite for nest excavation by most species of woodpecker. While the characteristics of snags utilized by woodpeckers for nesting have been studied widely, relatively little is known about structures associated with foraging (Bull and others 1997, Conner and others 1994, Steeger and others 1996). Moreover, the potential influences of foraging

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woodpeckers on snag decomposition characteristics, and therefore subsequent nest site quality, have gone largely unexplored.

In the interior ponderosa pine forests of the western United States, woodpeckers are commonly associated with dead or dying trees where they feed upon bark and wood boring beetles. In their search for prey, they puncture bark surfaces and fragment the underlying wood, thereby altering local microhabitat conditions. Otvos (1979) suggested that such behavior may actually expedite the process of snag decay by creating vectors for the colonization of wood decay organisms. Additionally, Conner and others (1994) observed that hardwood snags which received relatively more foraging activity by woodpeckers tended to have higher incidences of decayed wood. Considering that most species of woodpecker in North America require some form of wood decay for nest excavation, potential interrelationships between foraging activities and the spread of decay fungi in snags are intriguing.

Because organisms that promote sapwood decay tend to rapidly colonize dying conifers (Harmon and others 1986, Mercer 1982, Rayner and Boddy 1988), early patterns of snag utilization are likely central to understanding the relationship between woodpecker use and subsequent decay dynamics. Several researchers have reported concentrated foraging activity by some woodpecker species within the first few years of tree death (Bull 1983, Bull and others 1986, Murphy and Lehnhausen 1998, Steeger and others 1996). However, few have quantified foraging intensity across a spectrum of decay classes, or elucidated the relationships between foraging woodpeckers and subsequent snag decay dynamics.

Addressing such ecological questions requires the use of large populations of known age snags. Consequently, researchers often rely on snags produced in naturally occurring perturbations such as wildfires, insect outbreaks, or windthrow events, but this may prove problematic in many cases because the exact time and mode of death may be attributed to several underlying sources. Because the biological decay activity of a tree is directly related to both the timing and cause of its demise, it is easy to envision how controlling these two variables can greatly aid in the reduction of long term error. In this study, we made use of an experimental population of snags intentionally infested with bark beetles (using pheromone baits) as part of a separate, long-term entomological study. As a result, the exact date and mode of mortality were known, which narrowed the range of possible decay pathways and permitted us to better examine the effects of foraging woodpeckers on subsequent snag decay processes.

The purpose of this research was to investigate the dynamic relationship of foraging woodpeckers and ponderosa pine decay. Specifically, we wanted to identify the structural changes in ponderosa pine throughout the decay sequence, determine the decomposition stages used most intensely by foraging woodpeckers, and examine the effect of these foraging activities on sapwood decomposition.

Study Area and Methods

The study was conducted on three National Forests in the Cascade Range: the Lassen located in northeastern California and the Ochoco and Deschutes National Forests in central Oregon *(fig. 1)*. Interior ponderosa pine *(Pinus ponderosa* var. *ponderosa)* was the dominant species at all three locations. The Oregon sites had a minor component of both Douglas-fir *(Pseudotsuga menziesii)* and white fir *(Abies* *concolor* var. *lowiana),* while the higher elevations of the Lassen site contained a large component of Jeffrey pine *(Pinus jeffreyi),* with scattered inclusions of white fir and incense-cedar *(Libocedrus decurrens).* Elevations ranged from 2,275 meters on the Ochoco National Forest to 2,730 meters on the Lassen National Forest. Resident woodpecker species of interest included the white-headed *(Picoides albolarvatus),* downy *(P. pubescens)* three-toed *(P. tridactylus),* black-backed *(P. arcticus),* hairy *(P. villosus),* and pileated woodpeckers *(Dryocopus pileatus).* Other woodpecker species (i.e., northern flicker *[Colaptes auratus]* and three species of *Sphyrapicus* sapsuckers) were also present, but do not typically feed on decaying pines.

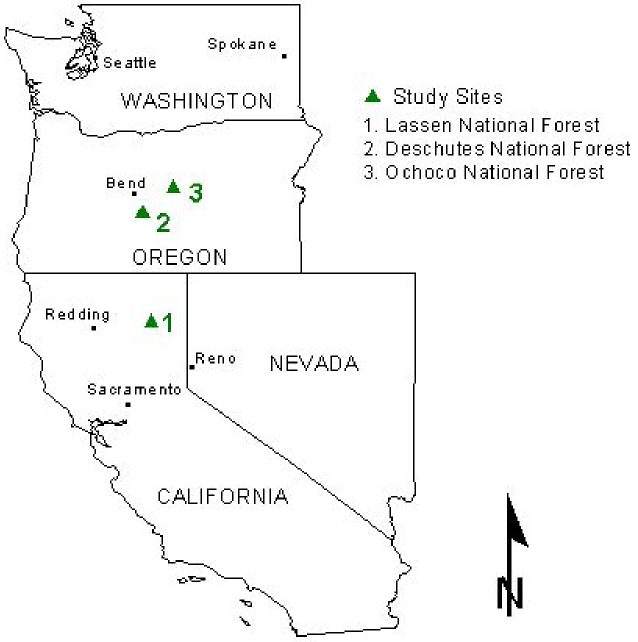

Figure 1—The three snag data collection areas in central Oregon and northeastern California.

Methods

Because snag decomposition is a slow and variable process, charting structural and biological changes directly requires very long periods of time. One recognized alternative is to use a chronosequence of snags with known dates of origin for reconstructing temporal patterns of decay. Between the three forests, we developed a chronosequence consisting of 144 snags ranging in age from 1 to 9 years. Snags on the Ochoco and Deschutes sites were created by bark beetles responding to pheromone baits in 1998 and 1997, respectively. Snags on the Lassen site were sampled from two separate populations. Half were baited with bark beetle pheromone in 1993 and the remainder were sampled from a large population of naturally occurring snags with known ages. All 144 snags, which ranged from 40 to 130 centimeters in diameter, were sampled between 1 June and 31 August 1999.

To document structural and biological changes in the snags across the chronosequence, seven age-dependant variables were visually recorded. These included: foliage color (green, lime green, yellow, red), foliage retention (expressed as percent of needles remaining), bark retention (expressed as percent remaining), bark integrity (tight or loose, as indicated when the bark was punctured), presence of woodpecker nest cavities, presence of bark beetle pitch tubes, and type and quantity of beetle exit holes. Because the phenology of beetles foraging on ponderosa pine follows a distinct chronology, the size and shape of holes left in the bark when beetles exit the snag are indicative of particular families, and are therefore useful indicators of decay progression (Patrick J. Shea, pers. comm.). Using this information, we were able to classify and quantify exit holes of three taxonomic families in chronological order of tree infestation: Scolytidae ("primary" invaders), Buprestidae ("secondary" invaders), and Cerambycidae ("secondary" invaders).

To compare woodpecker foraging activity across snag ages, we developed a foraging intensity index based on the cumulative number of foraging excavations per square meter. Foraging intensity was quantified on each snag using a 30x spotting scope and counting all visible foraging excavations from a distance of 30 meters on a randomly selected azimuth. Counts were cumulative and did not distinguish between current season and previous years' foraging evidence. The surface area surveyed was calculated and divided into the number of observed foraging "hits," resulting in a standardized index of foraging hits per square meter of snag surface.

As a relative indicator of sapwood softness, we used a six-joule Proceq Pilodyn wood tester (Crown 1978, Sprague and others 1983). The Pilodyn compresses a spring loaded steel pin into the sapwood with a constant force, measuring penetration depth in millimeters. On each snag, at a height of 1.3 meters, we removed a square piece of bark measuring 4 centimeters^2 at each of the four cardinal directions. This permitted the Pilodyn direct access into the sapwood, which was measured with the Pilodyn three times at each exposed site to compute an average penetration in millimeters for 12 strikes per snag. Before bark removal, we quantified woodpecker foraging within the immediate area by counting foraging hits in a 15x15 centimeter area.

Because snags were sampled from two differing sources (bark beetle killed and unknown mortality causes) and considering that the mode of tree death likely influences subsequent woodpecker foraging activity and decay dynamics, we divided the data into two subsets, based on mortality agent, prior to analysis. We used simple linear regression to evaluate the relationships between woodpecker foraging, and both snag age and sapwood softness.

Results

Visual decay characteristics changed directionally with increasing snag age along the chronosequence *(table 1).* In general, foliage color tended to turn from dark green to lime or yellow within the first year and was red by year 2. Needle retention dropped to an average of 85 percent within the first year and 14 percent by year 2. By year 3 all snags had completely lost their foliage. Bark retention was 100 percent until year 4, then fell to between 90 and 95 percent for the remainder of age classes. However, 50 percent of the sampled snags had loose or sloughing bark by year 4 and all snags had loose bark by age 6.

Table 1—*Structural decay characteristics of 144 ponderosa pine snags across 10 age classes in the central and southern Cascades of Oregon and northeastern California, 1999.*

Snag	Mean/std. dev. age class			Percent of age class exhibiting described feature					
Age	Foliage	Pct needles	Pct bark	Loose	Pitch	Exit holes			Nest
Class	Color[1]	Remaining	Remaining	Bark	Tubes	Scolytidae	Buprestidae	Cerambycidae	Cavities
0	Green	100/0	100/0	0	0	0	0	0	0
1	Lime	85/23	100/0	0	97	93	71	0	0
2	Red	13.5/24	100/0	0	92	100	90	23	0
3	n/a	0/0	100/0	50	75	100	100	100	50
4	n/a	0/0	95/5	71	75	100	100	100	50
5	n/a	0/0	90/7	75	50	100	100	100	50
6	n/a	0/0	90/19	100	50	100	100	100	71
7	n/a	0/0	90/0	100	50	100	100	100	100
8	n/a	0/0	90/14	100	50	100	100	100	100
9	n/a	0/0	90/29	100	13	100	100	100	100

[1] Color means calculated using 1 = green, 2 = lime, 3 = yellow, 4 = orange, and 5 = red.

The presence of beetle pitch tubes, which indicates either past or present beetle infestation, was highest during the first year, with 97 percent of sampled snags exhibiting tubes. This proportion gradually decreased over time, with only 13 percent of the snags having old tubes remaining by age 9. Ninety-three percent of 1-year-old snags exhibited exit holes created by members of the family Scolytidae, and this figure increased to 100 percent by the second year. Secondary beetles of the families Buprestidae and Cerambycidae emerged during the first and second years, respectively. Ninety percent of 1-year-old snags had Buprestid exits, but no visual evidence of Cerambycid emergence. By the second year, 100 percent of the snags showed signs of Buprestid emergence, while Cerambycid beetles emerged from only 23 percent of the snags. By the third year, 100 percent of the snags showed evidence of both beetle families. Nest cavities showed up in 50 percent of the snags by the third year, 71 percent by year 6, and all snags had cavities by year 7.

Initial linear regression analysis revealed no significant increase in woodpecker foraging intensity between beetle killed snags and those with unknown causes of mortality. Additionally, because t-test comparisons revealed similar slopes for each set ($p = 0.001$), the two data sets were combined for all subsequent analyses. Further regression analysis on the entire set of snags yielded similar results, with no increase in woodpecker foraging intensity as snags aged *(fig. 2)*. The slope of the regression line did not significantly differ from zero ($p < 0.0001$), indicating that most woodpecker foraging activity took place in the early stages of decay. Sapwood softness was not linearly related to the amount of woodpecker foraging *(fig. 3)*.

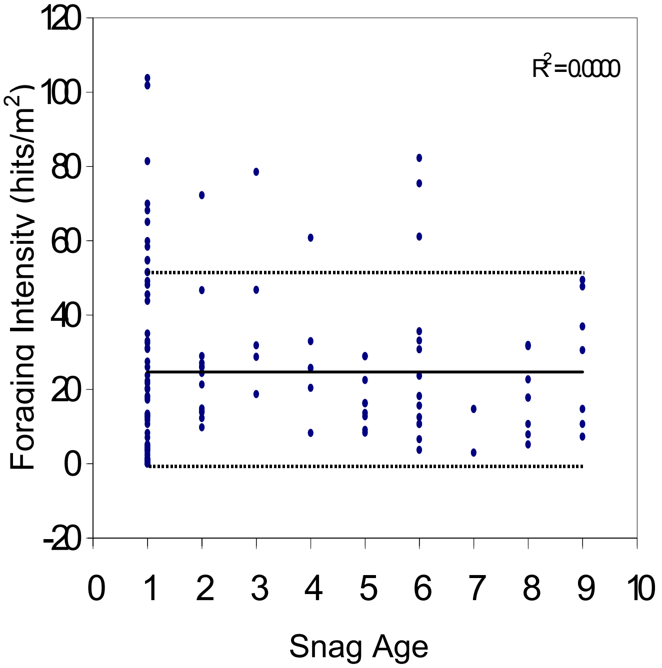

Figure 2—Linear regression analysis of cumulative woodpecker foraging intensity and snag age from 144 snags sampled on the Deschutes and Ochoco Forests in central Oregon and the Lassen National Forest in northeastern California, 1999. Dashed lines indicate 95 percent confidence intervals.

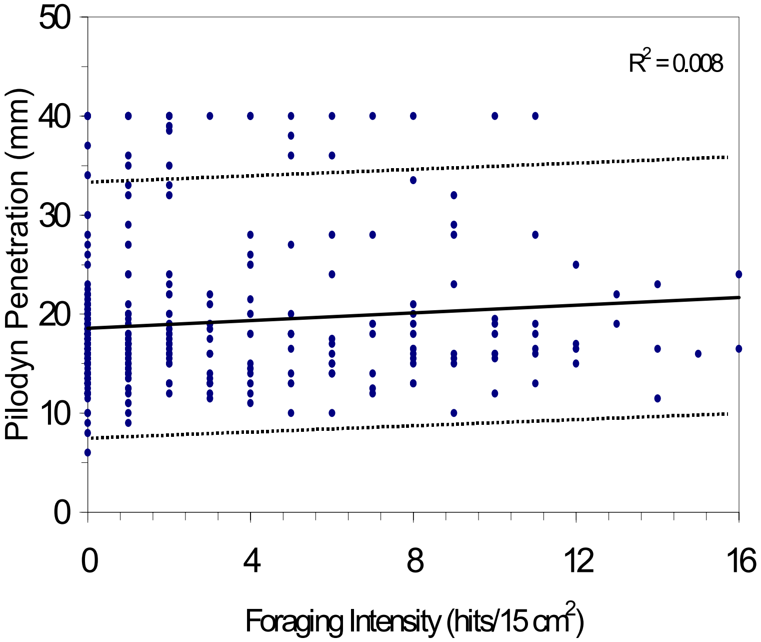

Figure 3—Linear regression analysis of woodpecker foraging intensity and sapwood softness as indicated by pilodyn penetration measured from 144 snags sampled on the Deschutes and Ochoco Forests in central Oregon and the Lassen National Forest in northeastern California, 1999. Dashed lines indicate 95 percent confidence intervals.

Discussion

The decay characteristics exhibited in this snag population show similarities with those described by other authors (Bull 1983, Raphael and Morrison 1987, Steeger and others 1996). However, we discretely defined snag decay characteristics to better reflect their value to foraging woodpeckers. For example, the commonly used decay classifications put forth by Thomas and others (1979) and Steeger and others (1996) broadly categorize snags on the basis of bark retention, needle, twig, and branch presence. Although these classifications are useful for defining suitable nest substrates, they probably do not reflect the more subtle changes in woodpecker foraging value resulting from early fluctuations in arthropod populations. We found that needleless snags were generally only 3 years old and would fit into decay category 1 (first category under "dead"), using established classification systems (Bull and others 1997, Steeger and others 1996, Thomas and others 1979). However, examination of beetle phenology data from our study areas (using exit holes as guidelines) suggests that most 3-year-old snags are probably past the peak of bark and wood boring beetle activity, and therefore less likely to be used by foraging woodpeckers. Consequently, a highly valuable foraging stage may be masked by current classifications. Maintaining high quality woodpecker foraging habitat may require modifications of current snag classifications to account for early stages of snag decay.

Woodpeckers in the study areas appear to concentrate their foraging activity within the first few years of tree death. This period coincides with the densest populations of bark and wood boring beetles, as evidenced by the appearance of beetle exit holes. These findings agree with what is currently known about the diets of *Picoides* woodpeckers that specialize on bark and wood boring beetles (Otvos 1965, 1970, 1979). Similar temporal foraging patterns have been documented in the literature (Bull 1983, Bull and others 1986, Parks 1999, Steeger and others 1996), especially in areas of epidemic beetle outbreaks (Amman 1984, Baldwin 1960, Kroll and Fleet 1979, Otvos 1965), or as a response to a localized perturbation such as windthrow (Wickman 1965) and fire (Murphy and Lehnhausen 1998).

Although these data appear to reinforce the notion that foraging woodpeckers concentrate their use on younger snags, it is based on a chronosequence of snag decay. Substituting space (in the sense of different geographical areas or individual snags) for time requires an inherent assumption regarding the temporal pattern of the foraging activity. When we sampled older snags, we assumed that the visible foraging sign took place in the early stages of the tree's demise. This may be a reasonably safe assumption considering the rapid, abundant, response of both beetles and woodpeckers to a dying tree. In general, the activities of both groups within the early stages of tree death is so intense, it numerically overwhelms further evidence of subsequent beetle-woodpecker activities. However, because each individual snag was not followed yearly from death, we cannot unequivocally determine at what point along the decay sequence the foraging took place. To gain accurate insight into the relationships between foraging woodpeckers and snag decay, it is critical to have a long term data set in which each snag is followed and woodpecker foraging is quantified yearly from the time of death. We hope to rectify this problem over time as our data set grows, but until then these results should be interpreted accordingly.

Finally, these data did not reveal any pattern between the intensity of woodpecker foraging and the relative degree of sapwood decay. There could be several explanations for this particular finding, two of which relate to the use of the

Pilodyn as a sampling tool, and one that has to do with woodpecker foraging ecology. First, in addition to the effects of climate, aspect, and microhabitat differences, live trees compartmentalize invading bacteria and fungi, thus isolating these organisms to localized areas, creating a patchy mosaic of sound and decayed wood (Shigo 1984). Our survey methods were only designed to measure sapwood decay in one small localized, radial area, but as demonstrated by Shigo (1984), wood decay is spatially variable in nature, thereby making our measures with the Pilodyn a hit or miss procedure. This is evidenced by the often highly variable Pilodyn readings even within a small, 1 cm^2 area. Although one measure may have hit sound wood, another just a few millimeters away might have produced a clearly decayed reading. Our selected method of decay quantification was somewhat limited considering this fine-scale variability.

A second possible reason for our inability to detect a relationship between woodpecker foraging intensity and sapwood decay could be explained by a phenomenon known as “case hardening.” Mercer (1982) noted that the outer 3-4 centimeters of sapwood is frequently harder than more interior points due to weathering and drying of the snag surface. The Pilodyn had a maximum extension of 40 millimeters. Consequently, it may not even have been penetrating the truly soft areas of the wood. It is clear that the Pilodyn has limitations for this purpose, yet several researchers have found Pilodyn measures comparable to those of specific gravity (Conner and others 1994, Sprague and others 1983) and wood density (Crown 1978). We are currently exploring various options to better detect and quantify relative sapwood decay on a more universal scale.

Finally, we believe that the foraging ecology of woodpeckers could have a marked effect on the dynamics of wood decomposition, thus affecting our ability to accurately quantify an interrelationship. Methods of food procurement differ between woodpecker species and could play a role in whether the wood is exposed to decay fungi. For example, several species of woodpecker are thought to predominantly “scale” for primary bark beetles, while others “excavate” for secondary wood boring beetles. Scaling behavior involves striking the bark at an angle to “scale” away the outer surfaces. This behavior rarely penetrates the wood, its purpose being to exploit food resources just under the bark’s surface. In contrast, excavation involves creating large holes into the bark and wood (usually in pursuit of wood boring organisms) which significantly alters the microhabitat of the sapwood. It is easy to envision how this excavation behavior might facilitate more rapid fungal colonization by providing greater access points into the snag’s interior.

Because particular species of woodpecker are thought to specialize in certain foraging behaviors, interspecific population dynamics in the area of an individual snag could alter the rates of sapwood fungal invasion. For example, the three-toed woodpecker generally forages using the scaling technique (Bull and others 1986, Murphy and Lehnhausen 1998), whereas species such as the hairy and black-backed woodpeckers are relatively stronger excavators (Bull and others 1986). If a given area had relatively larger populations of “scaling” species, then decay rates could be less pronounced due to the relatively minor substrate manipulations created by this foraging strategy.

These preliminary results offer some insights into the dynamic relationship of woodpecker foraging and ponderosa pine decay, yet our sampling methods need refinement to more accurately quantify the potential effect of foraging woodpeckers on snag decay processes. In particular, a better method of quantifying sapwood decay is needed. We are currently engaged in exploring these methodological issues and hope to further investigate the interactive biology of bark beetles, woodpeckers, and fungi in the decomposition of ponderosa pine.

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Forest Age and Relative Abundance of Pileated Woodpeckers on Southeastern Vancouver Island[1]

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Abstract

We estimated relative abundance of the pileated woodpeckers *(Dryocopus pileatus)* at four sites in the Coastal Western Hemlock Biogeoclimatic zone, on southeastern Vancouver Island during 1996-1997. The number of pileated woodpecker calls was correlated with age and structure of forests. Pileated woodpeckers did not use intensively managed forests < 80 years old that had low densities of dead wood (large snags and logs). They were most abundant in forests that had greater densities of dead wood and where 51 percent of the area was covered by >140-year-old stands. However, their abundance in these forests did not differ significantly from that in early seral forests (49 percent > 80-year-old stands) or old forests (70 percent > 140-year-old stands).

Introduction

The pileated woodpecker *(Dryocopus pileatus)* is an important species in forests of North America because, as a primary cavity nester, it creates habitat opportunities for secondary cavity nesters. It is the largest extant woodpecker species in North America and, because of its size, excavates large cavities. Hence, many species benefit from its nesting and roosting activities (Bunnell and others 2002). Loss of structural elements (e.g., logs, snags, and trees with broken tops, scars, decay, or damage) has the most significant impact on pileated woodpecker habitat; forest fragmentation likely reduces population density and makes pileated woodpeckers vulnerable to predation as they fly between forest fragments (Bull and Jackson 1995).

We estimated relative abundance of pileated woodpeckers in relation to habitat types and stand characteristics in the Coastal Western Hemlock Biogeoclimatic zone on southeastern Vancouver Island. For our study, we define relative abundance as the number of responses (the number of pileated woodpeckers calling or drumming in response to a recording) received per call station within an area. Relative abundance can be used to infer the quality of the habitat for species, and differences in the

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abundance of bird species often reflect the availability of resources to them (Schoener 1968).

Our objectives were to estimate relative abundance of pileated woodpeckers in different seral stages and structure classes of forest stands and examine associations between habitat features and abundance of pileated woodpeckers. We hypothesized that the relative abundance of pileated woodpeckers increases as age of forest increases and as the amount of forest harvesting decreases. We also expected that landscapes with greater quantities of dead or decayed large forest structures (i.e., snags, defective trees, and logs) will have a greater abundance of pileated woodpeckers.

Methods

Study Area

We selected our study area on southeastern Vancouver Island because it has a population of pileated woodpeckers (determined from historical records [Campell and others 1990] and from pilot surveys), a range of forest conditions, and because commercial timber harvesting occurs in the region. Forest management for timber in each site ranged from 100 percent logged and 60-80 percent spaced in the early seral study site, 40 percent logged and 39 percent spaced in the mid-seral study site, 20 percent logged and 4 percent spaced in the mature study site, and 22 percent logged and 5 percent spaced in the mature/old study site. The study area is located within the Very Dry Maritime Coastal Western Hemlock Biogeoclimatic subzone (CWHxm) (Anonymous 1993). It has warm, dry summers and moist, mild winters (Green and Klinka 1994). Forests in the CWHxm subzone are coniferous, dominated by Douglas-fir *(Pseudotsuga menziesii),* western hemlock *(Tsuga heterophylla),* and minor amounts of western red-cedar *(Thuja plicata),* but some deciduous species such as red alder *(Alnus rubra)* and bigleaf maple *(Acer macrophyllum)* occur (Green and Klinka 1994).

Field Methods

We established four 1,450-ha study sites. Each study site encompassed an area equal to the home ranges of approximately two to three breeding pairs of pileated woodpeckers. Home range size was estimated to be 478 ha for individuals after young fledged in coastal western hemlock climax forests dominated by Douglas-fir (Mellen and others 1992). The four sites represented four landscapes that differed in seral stage and forest structure. The Hillridge site was a homogeneous, early seral forest with few snags and medium numbers of large logs remaining after cutting of the primary forest *(tables 1, 2).* Niagara was a mid-seral forest with abundant remnant large snags and logs. Sooke was a mixed forest with early and mid-seral forests and mature/old forests with abundant remnant large snags and logs. Rithet represented most closely an unlogged mature/old seral forest with abundant snags and a modest number of logs.

Table 1—*Percentage of forest stand age classes in four pileated woodpecker study sites on southeastern Vancouver Island.*

Study site	Early seral ≤ 60 years	Mid-seral 61-100	Mature 101-140	Mature/old >140	Non-forest
Hillridge	73	27	0	0	0
Niagara	47	22	14	13	5
Sooke	26	9	0	51	13
Rithet	22	5	3	70	1

Table 2—*Mean (± SE) or percent frequency of forest characteristics of four pileated woodpecker study sites on southeastern Vancouver Island, 1996-1997.*

	Study sites (n = plots)				
Characteristic	**Hillridge (10)**	**Niagara (19)**	**Sooke (20)**	**Rithet (10)**	***P***
Coarse woody debris (m^3 ha^{-1})	75 (± 19)	176 (± 33)	213 (± 39)	114 (± 34)	[1]0.11
Snag or defective tree basal area (m^2ha^{-1})	0.7 (± 0.2)	4.3 (± 1.3)	7.1 (± 1.4)	11.9(± 2.5)	[1]<0.01
Stem density (stems ha^{-1})	1,810 (± 818)	688 (± 154)	355 (± 110)	760 (± 130)	[1]<0.01
Structural stage (pct)					[2]<0.01
Shrub	0	26	0	0	
Pole/sapling	30	37	5	0	
Young forest	70	21	30	10	
Mature forest	0	16	40	60	
Old forest	0	0	25	30	
Successional stage (pct)					[2]<0.01
Pioneer or young seral	70	58	5	0	
Mature or overmature seral	10	21	15	10	
Young climatic climax	20	10.5	20	10	
Maturing climax, maturing climatic climax and disclimax	0	10.5	60	80	
Disturbance (pct)					[2]<0.01
Logging, thinning, or spacing	100	84	40	0	
Fire, wind, or edge	0	16	25	70	
None	0	0	35	30	
Elevation (m)	387 (± 21)	518 (± 13)	371 (± 33)	537 (± 42)	[1]<0.01

[1] Kruskal-Wallis comparison among four study sites.

[2] Chi-square test between two young study sites (Hillridge and Niagara pooled) and two older study sites (Sooke and Rithet pooled).

Transects and call stations were systematically located in each study site to ensure even coverage. Four or five transects about 4 km long were placed along an east-west line 800 m apart. Call stations were located every 400 m along those transects, giving approximately 40 call stations in each study site. We avoided placing transects along known habitat gradients that might influence bird abundance (e.g., a riparian corridor) and thereby bias the sampling procedure (Ralph and others 1995).

Call-playback Survey

Call-playback surveys were used to estimate the relative abundance of pileated woodpeckers in two of the study sites during mating season (March 1996) and in all four study sites during nesting (May to June 1996 and 1997) and post-fledging seasons (July to August 1996 and 1997). We defined relative abundance as the response rate, or the number of responses (the number of pileated woodpeckers calling or drumming in response to a recording) divided by the number of call stations.

At each call station, a taped recording of pileated woodpecker calls and territorial drums was played at 30-s intervals using a 3-volt cassette player amplified by a battery-powered, hand-held 12-volt sound horn (Radio Shack Genexxa).[5] We used a pileated woodpecker call-playback survey methodology following protocols from British Columbia (Anonymous 1996a) and the USDA Forest Service's Pacific Northwest Research Station (Raley and Aubry 1993). Upon arriving at a call station, two field assistants would listen quietly and wait for 60-s while looking in all directions. If there was no call, or drum, or observation of a pileated woodpecker, then the entire recording of four calls and four drums was played, followed by a 5-min wait. If there was a call, drum or observation, during the initial 60-s wait or during the recording, the recording was stopped while observers watched and listened. Mid-transect responses and second responses at call stations were recorded but not included in the final data set. Mid-call station responses were disregarded because call-playback can stimulate pileated woodpeckers to follow observers or to call repeatedly. Records of second birds were eliminated to standardize the surveys as counts of potential pairs instead of counts of individual birds.

Surveys were conducted in good weather, neither on windy days (enough wind to cause leaves and twigs to be in motion: Beaufort scale 3) nor rainy days (steady rain), to maintain standard conditions for audibility and allow comparisons among surveys. We reduced observer bias by training field assistants and rotating assistants among transects. The survey period was divided into mating, nesting, and post-fledging seasons, based on observed pileated woodpecker behavior during the study, and on studies in British Columbia, Oregon, and Washington (Aubry and Raley, pers. comm.; Bull and Jackson 1995; Campbell and others 1990).

We examined how responses per call station and variability changed as number of call stations increased during a survey to determine the optimum sampling effort needed to estimate the relative abundance of pileated woodpecker. All the analyzed responses were randomized to remove seasonal and daily biases.

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[5] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Habitat Characteristics

To quantify habitat characteristics of study sites, 0.4-ha habitat circular plots (35.7-m radius) were established along 4 or 5 call-back transects in each study site: 10 plots each in Hillridge and Rithet, 19 plots in Niagara, and 20 plots in Sooke. Heterogeneous study sites were sampled at twice the effort of more homogeneous study sites. Information about each habitat plot was recorded using the Ecosystem Field Form and procedures of Ministry of Forests and Ministry of Environment (Anonymous 1996b, Luttmerding and others 1990). The variables used for analysis included volume of coarse woody debris, basal area of snags and defective trees, tree stems per hectare, structural stage, successional stage, disturbance type, and elevation. Coarse woody debris was defined as fallen trees or pieces of such trees ≥ 20 cm in diameter that were not self-supporting (fallen or suspended). Snags and defective trees were defined as dead trees ≥ 20 cm in diameter at breast height (dbh) and trees ≥ 20 cm dbh with broken tops, scars, decay, or damage, respectively. Stem density was estimated for each plot by counting all stems > 3 m tall within a 5.64-m radius circle in the center of each plot, and then multiplying by 100.

Geographical information system (GIS) data (area of study sites, forest coverages, elevation, and aspect) about the sites were compiled from digital data prepared in 1991 and 1994 from aerial photographic interpretation and fieldwork conducted in 1986 and 1988. These data were updated to include changes in forest management activities and improvements in inventory classifications according to standards of the Ministry of Forests Inventory Branch.

Statistical Analysis

Data from call-playback surveys were analysed for statistical significance by using a logistic regression model. This model was appropriate because response data (whether a pileated woodpecker responded or not) were binary. Because all habitat data were non-normal, a non-parametric Kruskal-Wallis test was used to test for the differences in the dispersion of ratio habitat data from groups of more than two samples by ranking the data (Norušis 1998, Zar 1996). A Mann-Whitney U-test was used for ratio data to determine the differences between the dispersion of two groups (Sokal and Rohlf 1981, Zar 1996). For nominal habitat data, a Chi-square cross tabulation was used to test for the hypothesis of independence of the rows and columns of a contingency table (Norušis 1998, Siegel and Castellan 1988, Zar 1996).

The level of significance utilized for table-wide comparisons was $\alpha = 0.05$. A Bonferroni correction was used for multiple comparison tests.

Results

Determination of Adequate Sample Size

The optimum sampling effort was determined from the three sites: Niagara, Sooke and Rithet *(fig. 1)*. As the number of call stations reached 15 to 20 in habitats at the three study sites on southeastern Vancouver Island, the response rate and standard deviation stabilized. The steady decline of variability in mean response rate over cumulative number of call stations demonstrated that our sampling effort of ≥ 37 call stations per study area was sufficient to determine relative abundance of pileated woodpeckers. The sampling effort is probably optimal at 15-20 call stations for this type of forest in this biogeoclimatic zone.

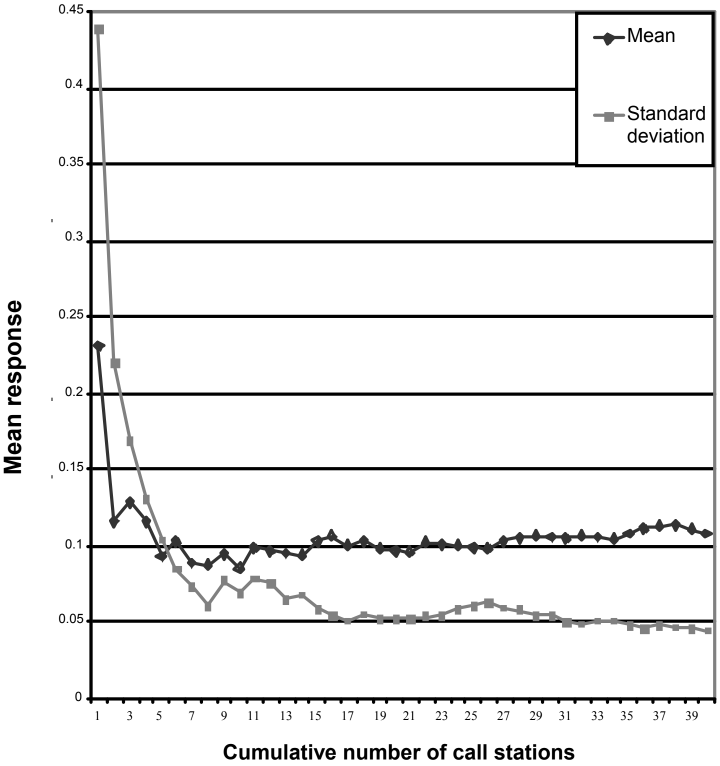

Figure 1—Mean response per call station using randomized data from 13 surveys in three pileated woodpecker study sites (Niagara, Sooke, Rithet) on southeastern Vancouver Island, 1996-1997.

Relative Abundance

A total of 16 call-playback surveys were conducted over two summers in 1996 and 1997. The lowest number of responses occurred in Hillridge: no responses in the nesting season and one response in the post-fledging season *(fig. 2).* Niagara and Sooke had greater mean responses per call station than Hillridge. Rithet was not significantly different than Hillridge, Niagara, or Sooke. Hillridge and Rithet were not surveyed during mating season due to logistical complications (snow).

The relative abundance of pileated woodpecker differed significantly overall among the study sites and differed significantly between some study sites:

Effect or contrast of variables:	***P***
All sites: average effect	0.01
Hillridge-Niagara	<0.01
Hillridge-Sooke	<0.01
Hillridge-Rithet	0.01
Niagara-Sooke	0.19
Niagara-Rithet	0.82
Sooke-Rithet	0.18
All seasons: average effect	0.17
Mating season-nesting season	0.14
Mating season-post-fledging season	0.06
Nesting season-post-fledging season	0.52

Thus, the likelihood of receiving a response of a pileated woodpecker to a transmitted call differed among sites; overall, the effect of site was significant (*P* = 0.01). Hillridge had the lowest relative abundance, in particular, during the nesting season when pileated woodpeckers were not detected during call-playback surveys. The likelihood of receiving a response in Hillridge was significantly lower than in the other study sites. Niagara and Rithet were the least different in abundance.

Sooke had the highest mean response rate of any study site for all three seasons. However, there was no significant difference in relative abundance of pileated woodpeckers between Sooke and Niagara. Niagara and Rithet also did not differ significantly. The effect of season on the likelihood of receiving a response of a pileated woodpecker was not significant (*P* = 0.17).

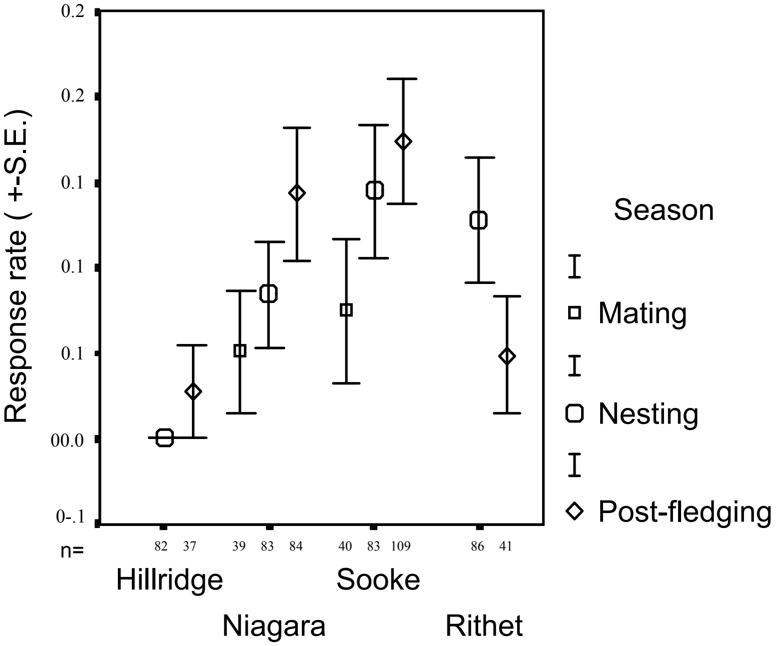

Figure 2—Relative abundance of pileated woodpecker at four study sites on southeastern Vancouver Island during three seasons, 1996-1997. Study sites are arranged from earliest to latest seral stage from left to right, n = number of call stations.

Habitat Characteristics of Study Sites

The study sites differed significantly for all habitat characteristics except coarse woody debris *(table 2)*. Coarse woody debris, however, was greater at Niagara and Sooke than at Hillridge and Rithet. Significant differences occurred for amount of snag and defective tree basal area, number of stems, structural stages, successional stage, disturbance, and elevation. The following tabulation gives the *P* values for these comparisons between areas:

	***P* values for habitat characteristics**	
Between site comparisons	**Basal area**	**Stem density**
Hillridge-Niagara	0.286	0.040
Hillridge-Sooke	<0.001	0.002
Hillridge-Rithet	<0.001	0.247
Niagara-Sooke	0.057	0.065
Niagara-Rithet	0.002	0.429
Sooke-Rithet	0.035	0.017

Although the statistical significance of differences among sites varied with individual habitat features, the four study sites can be characterized as follows. Hillridge consisted of pole/sapling and young forest structural stages, typical of mainly early seral forest. It had low amounts of coarse woody debris, a low basal area of snags, and it had the highest density of tree stems. The entire area was disturbed by logging, thinning, and spacing. Niagara was composed of several structural stages: shrub, pole/sapling, and young forest with a smaller amount of mature forest. Niagara had more seral stages than Hillridge and the coarse woody debris and basal area were greater than at Hillridge. The Niagara study site was disturbed by logging, thinning, or spacing.

Sooke had young forest, mature forest, and old forest structural stages but also had older seral stages. Amount of coarse woody debris and basal area of snags were greater than Hillridge or Niagara. Disturbance from logging was less than at Hillridge or Niagara sites. Rithet had structural stages similar to those at Sooke but with more mature and old structural stages and older seral stages. Amount of coarse woody debris was less than Niagara or Sooke, although the basal area of snags was greater than at other sites. The amount of disturbance was much less because none of the area was logged, thinned, or spaced.

Discussion

Our examination of the relative abundance of pileated woodpeckers in different seral stages has shown that there is not a direct correspondence between relative abundance and forest age. This occurs because both forest age and the quality of forest in terms of older wooden structures, both live and dead, appear to determine abundance of pileated woodpeckers. There was no significant difference in relative abundance of pileated woodpeckers among seasons, although relative abundance tended to increase in all study sites from nesting to post-fledging seasons probably because of the recruitment of juveniles. We accepted our hypothesis that landscapes with a significantly higher abundance of pileated woodpeckers have greater quantities of mature forest structures (snags, defective trees, logs).

The uniform young forest at Hillridge, < 80 years old, was not used by pileated woodpeckers during the nesting season and was used minimally during the post-fledging season. This low abundance may indicate that nesting sites were not available either within or close to Hillridge. The low abundance of pileated woodpeckers may also reflect that second-growth forests harvested before 80 years and then the cut blocks burned would likely lose old wooden structures important to pileated woodpecker, particularly for nesting. In Douglas-fir and western hemlock forests of western Oregon, the density of pileated woodpeckers was greater in forests > 80 years old than in forests < 80 years old (Nelson 1988). This suggests that intensive forest harvest that removes most residual old structures, could significantly reduce the relative abundance of pileated woodpecker for up to at least 80 years. Mannan (1984) found that pileated woodpeckers did not use forests < 40 years old for foraging and did not use forests < 70 years old for nesting.

There was no significant difference between the abundance of pileated woodpeckers in the mainly early- and mid-seral forest at Niagara and in the older forests at Sooke and Rithet. This may indicate that pileated woodpecker has some habitat flexibility in age of forest and in quality of that forest as expressed by residual old structures. This flexibility, however, should not be construed to mean that any early seral forest is acceptable habitat to pileated woodpeckers. All three study sites contained contiguous or residual patches of old forests or old forest structures. Without these late seral remnants, we expect that the abundance of pileated woodpeckers would differ among sites. On southern Vancouver Island, pileated woodpeckers do not require contiguous older forest, and their abundance is not significantly reduced in a mixed seral forest with abundant residual old wooden structures and patches of old forest (Hartwig 1999).

Although not statistically different than Niagara and Rithet, the relative abundance of pileated woodpeckers was highest in Sooke, the study site with the greatest amounts of dead wood. This suggests that the combination of large amounts of coarse woody debris, high basal areas of snags and defective trees, and low densities of stems were the most attractive habitat features to pileated woodpeckers.

The relative abundance of pileated woodpeckers at the Rithet study site decreased during the post-fledging season despite that its relative abundance during the nesting season was similar to Sooke's. The high basal areas of snags and defective trees may have provided suitable nesting sites, but the low amounts of coarse woody debris may indicate poorer foraging habitat.

Acknowledgments

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The Pileated Woodpecker as a Keystone Habitat Modifier in the Pacific Northwest[1]

Keith B. Aubry[2] and Catherine M. Raley[2]

Abstract

We propose that the pileated woodpecker *(Dryocopus pileatus)* is a keystone habitat modifier in the Pacific Northwest. It is the largest woodpecker in this region and the only species that forages primarily by excavating; only pileateds are capable of creating large cavities in hard snags and decadent live trees. A wide array of species, including many that are of management concern in the Pacific Northwest, use old pileated nest and roost cavities. In addition, pileateds provide foraging opportunities for other species, accelerate decay processes and nutrient cycling, and may facilitate inoculation by heart-rot fungi and mediate insect outbreaks. Because of the potential keystone role of pileated woodpeckers in Pacific Northwest forests, it may be appropriate to give special attention to their habitat needs in forest management plans and monitoring activities.

Introduction

A keystone species is an organism that has a significant influence on the ecosystem it occupies that is disproportionately large compared to its abundance or biomass (Power and others 1996, Simberloff 1998). In other words, a keystone is a relatively uncommon species that is functionally linked to the persistence of an array of other species and plays a critical role in the organization and/or functioning of the ecosystem. The term "keystone species" was first introduced by Paine (1966, 1969) to describe a starfish that maintained the organization of a rocky intertidal community by selectively preying on a mussel that would otherwise have been competitively dominant and prevented numerous other species from coexisting. Not all species that exert strong influences on an ecosystem are considered keystones; for example, the primary tree species in a forested ecosystem would be considered an "ecological dominant" rather than a keystone species, because its effects are a function of its importance in the ecosystem (Power and others 1996). Keystones may or may not influence ecosystem structure and function through trophic interactions, as in Paine's original example involving starfish and mussels; five broad categories of keystone species were described by Mills and others (1993), including keystone predators, prey, mutualists, hosts, and habitat modifiers.

The usefulness of the keystone species concept in ecology and conservation has been questioned recently (Mills and others 1993), but others (deMaynadier and

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Hunter 1994, Power and others 1996, Simberloff 1998) have argued strongly for its continued usage, largely because of its potential application to management and the conservation of biodiversity. Power and others (1996) suggested that if keystone species can be identified in threatened ecosystems, critical areas should be set aside to maintain keystones, rather than focusing management efforts solely on endangered species or "hot spots" of biodiversity. There is also concern that the current focus of ecosystem management on ecological processes, rather than on individual species, could result in a loss of biodiversity without detectable changes in key processes (Simberloff 1998, Tracy and Brussard 1994).

Simberloff (1998) argued that the conservation approach most likely to unite the best features of single-species and ecosystem management is to focus management efforts on keystone species because it involves explicit consideration of the mechanisms that underlie ecosystem function and structure. Unlike indicator, umbrella, or flagship species, keystones are functionally linked to a suite of other species; thus, management for the persistence of keystone species benefits other species by maintaining key ecosystem functions or structures. Furthermore, by studying keystone species and their role in ecological processes, we can significantly improve our understanding of ecosystems, identify ways to maintain or replace various functions, and increase the efficiency and success of conservation efforts.

The Pileated Woodpecker as a Keystone Habitat Modifier

Keystone habitat modifiers, also called "ecosystem engineers" (Lawton and Jones 1995), are species whose activities substantially alter the physical structure of the environment, influencing both available habitat for other species and various ecosystem processes (Mills and others 1993, Simberloff 1998). Examples include the beaver *(Castor canadensis),* because its dam-building and feeding activities create habitat for many other species and alter hydrological processes, channel geomorphology, biogeochemical pathways, and community productivity (Naiman and others 1986, Pollack and others 1995); the Brazilian termite *(Cornitermes cumulans),* because the large, abundant, and uniquely structured mounds it produces support a wide array of both obligate and opportunistic users (Redford 1984); and various species of burrowing animals, because their activities have a profound influence on available habitat for other species, and on microbial activity, soil fertility, the structure of plant communities, and sediment stability (Meadows and Meadows 1991).

We propose that the pileated woodpecker is a keystone habitat modifier in the Pacific Northwest, because the effects of its excavations on habitat for many other species and on various ecological processes are both large and unique. The importance of woodpecker cavities to a broad array of secondary cavity-using species (those that use cavities but do not create them) has long been recognized by ecologists and forest managers (Balda 1975, Conner 1978, Davis and others 1983, Neitro and others 1985, Thomas and others 1979), but the unique contribution of pileated woodpeckers to cavity creation and ecosystem function has received little attention (Machmer and Steeger 1995). To provide a focus for discussing management implications that may result from this designation, we have limited our evaluation of management prescriptions to those on USDA Forest Service lands administered under the Northwest Forest Plan (i.e., within the range of the northern spotted owl *[Strix occidentalis caurina]* in western Washington and Oregon and northwestern California; Anonymous 1994a, Tuchmann and others 1996).

The Ecological Role of Pileated Woodpeckers in the Pacific Northwest

Nesting, Roosting, and Foraging Requirements

The pileated woodpecker resides year-round in a variety of forested habitats. About the size of a crow, it is the largest woodpecker in the western United States, ranging from 40-49 cm in length and 250-350 g in body mass; males are 10-15 percent heavier than females (Bull and Jackson 1995). The pileated woodpecker is a primary cavity excavator and, because of its large size, selects correspondingly large (generally $\geq$65 cm d.b.h. in the Pacific Northwest) snags or live trees with heartwood decay for nesting and roosting. Pileateds generally occupy mid- to late-successional forests where such structures are abundant, but they also occur in younger forests with large remnant trees and snags. Their diet consists primarily of wood-dwelling ants and beetle larvae, but other insects, fruit, and nuts are eaten when available (Bull 1987). Pileated woodpeckers excavate new nest cavities each year and exhibit strong selection for nest trees on the basis of tree diameter and the structural quality of the wood. Trees containing relatively sound wood in the early stages of decay from heart-rot fungi are preferred, presumably because soft wood in advanced stages of decay cannot support the large nest cavities of pileated woodpeckers (Harris 1983). Before selecting a final nest site in the spring, pileated woodpeckers often excavate multiple cavity-starts (Bent 1939, Bull and Meslow 1988, Hoyt 1957, McClelland 1977). Cavity-starts we found in western Washington were in various stages of completion; several had dimensions similar to active nest cavities and others, though not as large, were deep enough to function as potential nesting or roosting habitat for some secondary users.[3] Pileateds roost individually at night or during inclement weather in hollow trees to reduce the incidence of predation and conserve heat; roost chambers are large and generally have multiple openings to provide escape routes from predators (Bull and Jackson 1995).

Creating Habitat for Secondary Cavity Users

Pileated woodpeckers provide nesting and roosting habitat for secondary cavity users through three processes: excavation of nest cavities and cavity-starts, excavation of openings into roost cavities, and foraging excavations. Over 20 species of secondary cavity users occurring in the Pacific Northwest have been documented nesting or roosting in old cavities or openings excavated by pileated woodpeckers *(table 1).* The common merganser, silver-haired bat, fisher, and American marten were included as species of concern in the Final Supplemental Environmental Impact Statement for management of late-successional forests within the range of the northern spotted owl (Anonymous 1994b); the bufflehead, flammulated owl, and Vaux's swift are on priority or sensitive species lists in Washington and Oregon (Anonymous 1995, Marshall 1992); and the northern flying squirrel is a primary prey of the northern spotted owl (Forsman and others 1984).

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[3] Unpublished data on file, Pacific Northwest Research Station, Olympia, Wash.

Table 1—*Bird and mammal species known to use cavities, entrance holes, or foraging holes excavated by pileated woodpeckers in coniferous forests of the western U.S. and Canada. All species listed occur within the management area of the Northwest Forest Plan (Anonymous 1994a).*

Species	Location
Wood duck (*Aix sponsa*)	Western Montana, western Washington [1, 2]
Common goldeneye (*Bucephala clangula*)	Western Montana, Alberta [1, 3]
Bufflehead (*Bucephala albeola*)	Western Montana, Alberta [1, 3]
Hooded merganser (*Lophodytes cucullatus*)	Western Montana [1]
Common merganser (*Mergus merganser*)	Western Montana [1]
American kestrel (*Falco sparverius*)	Western Montana [1]
Flammulated owl (*Otus flammeolus*)	Northeastern Oregon [4]
Western screech-owl (*Otus kennicottii*)	Western Montana [1]
Northern pygmy-owl (*Glaucidium gnoma*)	Western Montana [1]
Boreal owl (*Aegolius funereus*)	Western Montana, central Idaho [1, 5]
Northern saw-whet owl (*Aegolius acadicus*)	Western Montana, western Oregon, western Washington [1, 6, 7]
Vaux's swift (*Chaetura vauxi*)	Northeastern Oregon, western Washington [7, 8]
Hairy woodpecker (*Picoides villosus*)	Western Montana [1]
Northern flicker (*Colaptes auratus*)	Western Montana, eastern Oregon, western Washington [1, 9, 7]
Brown creeper (*Certhia americana*)	Western Montana [1]
Silver-haired bat (*Lasionycteris noctivagans*)	Northeastern Oregon [10]
Big brown bat (*Eptesicus fuscus*)	South-central British Columbia [10]
Douglas' squirrel (*Tamiasciurus douglasii*)	Western Washington [7]
Red squirrel (*Tamiasciurus hudsonicus*)	Western Montana, northeastern Oregon [1, 8]
Northern flying squirrel (*Glaucomys sabrinus*)	Western Montana, northeastern Oregon, western Washington [1, 8, 7]
Bushy-tailed woodrat (*Neotoma cinerea*)	Northeastern Oregon [8]
Ringtail (*Bassariscus astutus*)	West-central Oregon [11]
American marten (*Martes americana*)	Western Montana, northeastern Oregon [1, 9]
Fisher (*Martes pennanti*)	Southwestern Oregon [12]

[1] McClelland 1979, [2] Bottorff 1999, [3] Bonar 1997, [4] Bull and others 1990, [5] Hayward and others 1993, [6] Mellen 1999, [7] Unpublished data, [8] Bull and others 1992, [9] Bull and others 1997, [10] Betts 1999, [11] Farrell 1999, [12] Aubry and others 1997.

Several characteristics of pileated woodpeckers and the cavities they excavate are unique among woodpeckers in the Pacific Northwest. Both the entrance hole and nest cavity of pileated woodpeckers are larger than those of other woodpeckers *(table 2)*; thus, pileated excavations may provide the majority of suitable tree cavities for larger mammals and birds. For example, in southwestern Oregon, female fishers typically used old pileated woodpecker cavities for natal den sites (Aubry and others 1997); based on our field observations and video taken at den sites, fishers would be unable to enter tree cavities with smaller openings. In northeastern Oregon, flammulated owls preferred pileated woodpecker cavities over flicker cavities for nest sites, possibly due to the larger cavity size and higher placement of the cavity in the tree bole (Bull and others 1990). In central Idaho, 18 of 23 boreal owl nests found were in pileated woodpecker cavities (Hayward and others 1993). Because boreal owls need large cavities and appear to prefer relatively high nest sites, Hayward and others (1993) recommended that management for boreal owl nesting habitat include management provisions for pileated woodpeckers. Eastern gray squirrels *(Sciurus carolinensis)* and raccoons *(Procyon lotor)* were observed using red-cockaded woodpecker *(Picoides borealis)* nests after the entrance and cavity were enlarged by pileated woodpeckers (Dennis 1971), and in British Columbia, buffleheads nested in cavities that had greater volume and larger entrance holes than those used by smaller secondary cavity-nesting species (Peterson and Gauthier 1985). In addition, some species may lay bigger clutches in cavities that have a larger floor area (Rendell and Robertson 1989).

Table 2—*Average dimensions of nest cavities for 12 woodpecker species occurring within the management area of the Northwest Forest Plan (Anonymous 1994a). Data are compiled from Terres (1980) except where noted.*

	Entrance hole size (cm)	**Cavity depth (cm)**	**Cavity width (cm)**
Species with broad distributions within the management area of the Northwest Forest Plan:			
Pileated woodpecker [1]	9.0 x 12.0	57	21
Northern flicker [2]	6.3 x 7.0	30	15
Hairy woodpecker	3.8 - 5.0	25 - 38	?
Red-breasted sapsucker (*Sphyrapicus ruber*)	3.1 - 3.8	35	?
Downy woodpecker (*Picoides pubescens*)	3.1	20 - 30	?
Species with limited distributions within the management area of the Northwest Forest Plan:			
Lewis' woodpecker (*Melanerpes lewis*) [3]	5.0 - 7.6	23 - 76	13 - 20
Black-backed woodpecker (*Picoides arcticus*)	3.8 - 5.0	25	?
White-headed woodpecker (*Picoides albolarvatus*) [4]	3.8 - 5.0	20 - 38	9 - 13
Acorn woodpecker (*Melanerpes formicivorus*) [5]	4.0	22 - 70	15
Species whose distribution is primarily east of the Cascade crest:			
Three-toed woodpecker (*Picoides tridactylus*)	3.8 - 5.0	25	?
Williamson's sapsucker (*Sphyrapicus thyroideus*) [6]	4.2	20 - 27	9 - 13
Red-naped sapsucker (*Sphyrapicus nuchalis*)	3.1	20	10

[1] Bull 1987, [2] Erskine and McLaren 1972, [3] Tobalske 1997, [4] Garrett and others 1996, [5] Koenig and others 1995, [6] Dobbs and others 1997.

In the Pacific Northwest, pileated woodpeckers typically locate nest cavities high in the bole of both snags and live trees (Aubry and Raley 1995, Bull 1987, Madsen 1985, McClelland 1979, Mellen 1987). Several studies have suggested that nest cavities located high off the ground may reduce the incidence of nest predation. Observed predation by raccoons on yellow-bellied sapsucker *(Sphyrapicus varius)* nests was attributed to the cavities being too shallow or too close to the ground (Kilham 1971), and higher cavities increased the reproductive success of tree swallows *(Tachycineta bicolor)* by reducing the probability of predation (Rendell and Robertson 1989).

Pileated woodpeckers are strong excavators capable of creating nest cavities in sound wood of both snags and live trees (Bull 1987, Christy 1939, Harris 1983). The sill width (an indicator of cavity wall thickness) of nest cavities in northeastern Oregon averaged 6 cm (Bull 1987), and two cavities we measured in western Washington had sill widths of 5.7 and 6.9 cm.[3] The sills of yellow-bellied sapsucker and northern flicker cavities in central British Columbia averaged 5.1 and 1.9 cm, respectively (Erskine and McLaren 1972), suggesting that pileated woodpecker cavities may have thicker walls than those of other woodpeckers. Thicker cavity walls decrease the rate of thermal conduction, which increases heat retention within the cavity (Betts 1998, Desch and Dinwoodie 1996, McComb and Noble 1981). In addition, cavities surrounded by a thick shell of sound sapwood provide better protection from predators, such as raccoons and black bears *(Ursus americanus)* that climb trees and break open nest cavities (Conner 1977, Conner and others 1976, Daily 1993, Erskine and McLaren 1972, Kilham 1971). These characteristics also increase the structural integrity of the cavity and reduce the likelihood that the tree will break at the cavity (Bull 1987, Harris 1983). Thus, nest cavities and cavity-starts excavated by pileated woodpeckers may provide more protection from potential predators, have greater longevity, and provide habitat for secondary users over a longer period of time than those excavated by other woodpeckers.

Hollow chambers in snags and live trees, which are created by the process of heartwood decay, are important to a wide array of bird and mammal species for nesting, roosting, denning, and resting (Bull and others 1997). Openings excavated into hollow trees by pileated woodpeckers for roosting enable secondary cavity users to access tree hollows they would otherwise be excluded from (i.e., the tree does not have a broken top or other natural openings that provide access to the hollow interior). In northeastern Oregon, radio-tagged pileated woodpeckers used an average of seven roost trees within a 3-10 month period (Bull and others 1992). In western Washington, pileateds also used an average of seven roost trees during an 8-month period, and one individual used 29 different roost trees during the 3 years we radio-tracked it.[3] However, because birds were not tracked daily in either study, the actual number of roost trees used by pileated woodpeckers each year is probably much higher. For each individual to have an adequate number of roost sites within its territory, it would need to excavate openings into several new roost sites each year. Thus, tree cavities that are used as nesting, roosting, and resting sites by other species are being created or made available by pileated woodpeckers throughout the year.

Lastly, the foraging excavations of pileated woodpeckers may also create important microhabitats for other species. Pileateds excavate deep into heartwood to reach carpenter ants (*Camponotus* spp.). These excavations may create openings into the decaying bole of snags and live trees that provide access to hollow chambers that are used by other species for nesting or roosting. For example, in south-central

British Columbia, a maternal colony of big brown bats was located in the hollow interior of a ponderosa pine *(Pinus ponderosa)* snag that they accessed through an opening created by a foraging pileated woodpecker (Betts 1999). Furthermore, foraging excavations that do not access hollow chambers can still be deep enough to provide roosting habitat for smaller cavity-users, such as the hairy woodpecker and brown creeper (McClelland 1979).

Providing Foraging Opportunities for Other Species

The pileated woodpecker is the only species that excavates extensively into sapwood and heartwood for invertebrate prey. Other Pacific Northwest woodpeckers are relatively weak excavators that typically locate prey by scaling bark, pecking substrates without penetrating the subcambial layers, surface gleaning, ground foraging, or hawking (Bull and others 1986; Conner 1979, 1981). Thus, pileated foraging excavations enable other species to prey on invertebrates that would otherwise be unavailable to them. Downy and hairy woodpeckers have been documented following foraging pileateds and gleaning or pecking in freshly excavated areas as soon as the pileateds leave (Bull and Jackson 1995, Christy 1939, Maxson and Maxson 1981).[3] Commensal foraging has also been observed between pileated and red-bellied woodpeckers *(Melanerpes carolinus),* northern flickers, and Williamson's sapsuckers (Bull and Jackson 1995).

Accelerating Decomposition and Nutrient Cycling

Pileated woodpeckers directly and indirectly accelerate wood decomposition and, ultimately, nutrient cycling by physically breaking apart sound and decayed wood as they excavate nest and roost cavities and forage for invertebrate prey and by exposing wood in live trees, snags, and logs to insect attack and fungal infection. Although pileated woodpeckers will obtain food by other methods, they are primarily excavators (Bull and Holthausen 1993, Bull and Jackson 1995, Conner 1979). A single foraging excavation can be large, often measuring 10-20 cm wide, >30 cm long, and extending deep into the heartwood (Christy 1939). One bird observed for 2 hours excavated two holes 15-cm deep with openings 15 x 15 cm and 15 x 25 cm in size (Christy 1939). In coastal forests of western Washington and Oregon, pileated woodpeckers forage mainly on standing dead and live trees, and only occasionally on downed logs (Aubry and Raley 1992, Mellen 1999); this differs from observations made by Bull (1987) in northeastern Oregon, where logs comprised a major proportion (36 percent) of foraging substrates used by pileateds. Thus, pileateds may have a greater impact on the decomposition of standing wood in coastal regions of the Pacific Northwest than in interior areas.

Facilitating Inoculation by Heart-rot Fungi

When woodpeckers excavate in dead wood, they expose new sites to insect attacks and fungal infection; additionally, it has been suggested that woodpeckers may facilitate the inoculation of live, healthy trees by heart-rot fungi (Otvos 1979, Parks 1999). Wood softened by heart-rot is essential for nest-cavity excavation by most woodpeckers (Conner and others 1976, Daily 1993, Kilham 1971), and heartwood decay in live, standing trees is the process by which hollow chambers in both trees and logs are formed (Bull and others 1997). Airborne spores of heart-rot fungi invade living trees through wounds that expose the heartwood to infection (Bull and others 1997). Pileated woodpeckers are capable of creating cavities in live trees with no decay (Bent 1939, Harris 1983). Almost half of the cavity-starts we located in western Washington were in live trees, and most were deep enough to have penetrated the heartwood (Aubry and Raley 1992). Thus, it is possible that pileateds create wounds in healthy trees that become infection courts for heart-rot fungi.

Mediating Insect Outbreaks

The importance of woodpeckers in the control of insect populations, especially beetles, has long been recognized (Otvos 1979). Woodpeckers are adapted to forage on a variety of substrates and can access insect prey in the crevices of rough bark that are unavailable to other avian predators (Jackson 1979a). In addition, because most woodpeckers are non-migratory, they are the primary avian insectivores during the winter months (Jackson 1979b); predation on overwintering arthropods is believed to reduce the potential of population increases during the following year (Jackson 1979b, Kroll and Fleet 1979).

When woodpeckers scale bark or excavate into wood for insects, there are both direct and indirect effects on prey populations. Woodpeckers affect insect mortality rates through direct consumption. Indirect effects include altering insect microhabitats, increasing parasite densities, and exposing remaining prey to consumption by both vertebrate and invertebrate predators (Machmer and Steeger 1995, Otvos 1979). Woodpecker foraging physically alters tree and log surfaces by reducing bark thickness or removing bark and sapwood, potentially exposing remaining insects (particularly broods) to extreme temperatures and desiccation. These changes in microclimatic conditions can be significant mortality factors for beetles and other arthropods (McCambridge and Knight 1972, Otvos 1979). Woodpecker foraging activity changes bark color, which may also influence its thermal properties and suitability as arthropod habitat (Jackson 1979b). Scaling, by reducing bark thickness, exposes remaining insect broods to parasites with short ovipositors (Machmer and Steeger 1995, Otvos 1979). For example, in the central Sierra Nevada in California, parasites were observed swarming over sites that had recently been scaled by woodpeckers and ovipositing through the thinned bark layers (Otvos 1970).

Whether pileated woodpeckers have a greater impact on insect populations than other woodpeckers has not been investigated, but they are clearly the best-adapted species for digging larvae and pupae out of bark, sapwood, and heartwood, regardless of the stage of wood decay. Carpenter ants generally comprise >50 percent of pileated woodpecker diets (Beckwith and Bull 1985, Jackman 1975), but during outbreaks, beetles may comprise a higher percentage of the diet (Bull 1987, Kroll and Fleet 1979). In Texas, pileated, hairy, and downy woodpeckers significantly reduced numbers of overwintering pupae and brood adults of the southern pine beetle *(Dendroctonus frontalis)* (Kroll and Fleet 1979). We commonly found larval Coleoptera in pileated woodpecker scats in western Washington (Aubry and Raley 1996), and in Montana, pileateds commonly foraged on both carpenter ants and wood-boring beetles (McClelland 1979).

Implications for Management Under the Northwest Forest Plan

Regulations pursuant to the National Forest Management Act of 1976 require that each National Forest identify "management indicator species" (MISs) to focus management attention on a species, species group, or habitat element to improve resource production, population recovery, maintenance of population viability, or ecosystem diversity (Anonymous 1984). Prior to the implementation of the Northwest Forest Plan (NWFP) in 1994 (Anonymous 1994a), the pileated woodpecker was an MIS for mature and old-growth forest conditions on all National Forests currently managed under the NWFP. Each Forest was required to establish a series of pileated woodpecker habitat areas that included both tracts of mature and old-growth forest and minimum densities of large snags (Anonymous 1986). To evaluate the effectiveness of these habitat areas, monitoring of occupancy and population trends was also required (Anonymous 1982).

The Northwest Forest Plan represents an ecosystem management strategy designed to provide for long-term ecological integrity throughout the range of the northern spotted owl, and includes specific provisions for late-successional reserves in both upland and riparian areas, as well as the retention of snags for cavity-nesting birds in lands open to timber harvesting (matrix lands). With the implementation of the NWFP in 1994, pileated woodpecker habitat areas were no longer maintained on most National Forests within the range of the northern spotted owl because it was believed that standards and guidelines (S&Gs) in the NWFP were adequate to maintain viable populations of pileated woodpeckers on federal lands.[3] Standards and guidelines in the NWFP for green-tree, snag, and log retention in timber harvest units on matrix lands in Forest Service ownership are summarized in *table 3*. Monitoring is a key component of management strategies in the NWFP and includes three types: implementation monitoring to determine if S&Gs are being followed, effectiveness monitoring to determine if they are achieving desired results, and validation monitoring to determine if underlying assumptions are sound (Anonymous 1994a).

Because of the potential keystone role of the pileated woodpecker in the Pacific Northwest, it may be appropriate to give special attention to their habitat needs in forest management plans and monitoring activities. Standards and guidelines for green-tree retention in the NWFP were strongly influenced by the Species Analysis Team's recommendation to emphasize clumped green-tree and snag retention in harvest units (Anonymous 1994b). Because of safety concerns associated with retaining large, hard snags or decadent live trees in harvested areas (Hope and McComb 1994, Styskel 1983), the Team believed that retaining green trees in relatively large patches would provide the best opportunities for preserving such structures in harvest units (K. Aubry, personal observation). However, there are few data to indicate that pileated woodpeckers will use large snags in harvest units, regardless of their context. Several studies in western Washington and Oregon have documented nesting by smaller woodpeckers in both natural and artificially created snags in clearcuts (Chambers and others 1997, Mannan and others 1980, Morrison and Meslow 1983, Schreiber and deCalesta 1992, Zarnowitz and Manuwal 1985), but nesting by pileateds in remnant snags or decaying live trees in clearcuts has not been reported.

Table 3—*Key Forest Service standards and guidelines for retention of green trees, snags, and logs during timber harvest on matrix lands in the Northwest Forest Plan (Anonymous 1994a).*

Emphasize green-tree and snag retention in matrix management

- Retain at least 15 pct of the harvested area as green trees.
- Retain 70 pct of those green trees in aggregates 0.2-1.0 ha in size. Retain the remainder as dispersed structures, either as individual trees or aggregates <0.2 ha in size.
- To the extent possible, aggregates and dispersed retention should include the largest, oldest live trees, decadent or leaning trees, and hard snags occurring in the unit. Patches should be retained indefinitely.
- As a minimum, snags are to be retained within the harvest unit at levels sufficient to support species of cavity-nesting birds at 40 pct of potential population levels based on published guidelines and models.
- To the extent possible, snag management within harvest units should occur within the areas of green-tree retention.

Provide specified amounts of coarse woody debris in matrix management

- In western Washington and Oregon north of and including the Willamette National Forest, leave 240 linear feet of logs per acre ≥20 inches in diameter. Logs <20 feet in length cannot be credited toward this total. In western Oregon south of the Willamette National Forest, leave 120 linear feet of logs per acre ≥16 inches in diameter and 16 feet long.
- Decay class 1 and 2 logs can be counted towards these totals. Down logs should reflect the species mix of the original stand.

We do not know if pileateds will nest or roost in suitable snags or decadent live trees located within 0.2-1.0-ha retention patches, but available data are not encouraging. We could find only one study on the use of remnant patches in regeneration harvests by pileateds. Gyug and Bennett (1995) conducted surveys for nesting pileated woodpeckers in coniferous forests of southeastern British Columbia on three 160-ha study plots including a clearcut, a clearcut with remnant patches about 1 ha in size, and an intact forest; experimental treatments were applied 25-30 yr prior to the study. Five pileateds were detected in the unharvested control, but none was found in either the clearcut or patch-retention treatment. Thus, regardless of the number of snags specified in management models, it is uncertain whether harvested areas will provide nesting or roosting habitat for pileated woodpeckers prior to the reestablishment of late-successional forest conditions.

Implementation monitoring has involved field visits to 109 randomly selected harvest sites since 1996 (Alverts and others 1997, 1998, 1999). Although data presented in these reports indicate a high level of compliance with S&Gs overall (≥95 percent), compliance with green-tree and snag retention S&Gs was generally lower. Snag and green-tree retention S&Gs were a source of considerable confusion for project personnel during all 3 years of monitoring, due to differing interpretations of the S&Gs, lack of consensus on definitions, lack of data on snag levels needed to support species of cavity-nesting birds at 40 percent of potential population levels, and the difficulty of maintaining “legacy” trees when operators are commonly confronted with safety concerns and operational constraints.

Clarifying S&Gs for green-tree and snag retention and providing additional guidance on their implementation would ensure that timber harvest administrators share a common understanding of their intent relative to ecosystem management and possess reliable strategies for implementing them on the ground. Although compliance with most relevant S&Gs is documented thoroughly in implementation monitoring reports, many of the details that will influence both the short- and long-term habitat quality of harvest units for pileated woodpeckers are not. For example, no data are collected on the number of large snags or decadent live trees that were preserved in the unit, how many were in aggregated vs. dispersed green-tree retention areas, or how many snags were created from living trees to meet minimum snag requirements. The inclusion of such information in implementation monitoring activities would greatly improve our ability to evaluate the habitat quality of harvested areas for pileated woodpeckers and other species associated with late-successional forest conditions *(table 1).*

Effectiveness monitoring under the NWFP is currently focused on late-successional and old-growth forests, aquatic and riparian ecosystems, northern spotted owls, and marbled murrelets *(Brachyramphus marmoratus);* monitoring strategies for other late-successional species are still being developed (Mulder and others 1999). Because of the large number of potential species in the latter category, Noon (1999) recommended that a "focal species" approach be used, and suggested that the keystone species concept may be useful for selecting ecological indicators for the Northwest Forest Plan. Because of its potential role as a keystone species in the Pacific Northwest and its strong association with large snags and decadent live trees, the pileated woodpecker may be a particularly appropriate ecological indicator for effectiveness monitoring of species associated with late-successional forest conditions. Other issues to address in effectiveness monitoring might include the prevalence of new pileated woodpecker nest cavities in clearcuts and retention patches, the relative abundance of pileated woodpecker cavities and foraging excavations in different forest types and moisture regimes, and occupancy levels and population trends in managed vs. unmanaged landscapes.

Several studies have recently been initiated to test or re-evaluate some of the assumptions in the NWFP (Aubry and others 1999, Marcot and others 2002), but we are not aware of any new or planned field studies of pileated woodpeckers within the management area of the NWFP. When validation monitoring strategies for the NWFP are formalized, it may be appropriate to include empirical evaluations of S&Gs for green-tree and snag retention relative to the habitat needs of pileated woodpeckers and of the model used to develop habitat management prescriptions for pileated woodpeckers in westside forests (Neitro and others 1985, p. 141-145). Lastly, habitat management strategies for woodpeckers in the Pacific Northwest are based on the assumption that viable populations can be maintained in managed landscapes by providing nesting snags at 40 percent of potential population levels (Thomas and others 1979, p. 72), yet this assumption has never been evaluated empirically.

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Characteristics and Dynamics of Cavity Nest Trees in Southern British Columbia[1]

Christoph Steeger[2] and Jakob Dulisse[3]

Abstract

We report on the characteristics, persistence, and temporal use patterns of nest trees of cavity-nesting wildlife in coniferous forests of southern British Columbia, Canada. Our goal is to identify the types of trees required to be retained during forestry operations if viable populations of cavity nesters are to be maintained in managed forests. Between 1994 and 1999, we recorded nesting species and tree characteristics during the year of first detection of active nest trees and in subsequent years, to document changes in wildlife use and tree condition. We located a total of 602 nests of 16 cavity-nesting species in 420 trees. Predominant tree species with active nests were Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). More than half of all nest trees were dead and/or partially broken when first detected. Three to 4.5 percent of nest trees were lost due to uprooting or total breakage each year. Partial breakage occurred at average annual rates of 1.1 to 6.2 percent each year. During the study period, 30 percent of nest trees were reused by breeding cavity nesters.

Introduction

Trees suitable for cavity excavation are an essential resource for wildlife species that require cavities in trees for breeding, roosting, and shelter from inclement weather and predators. The suitability of trees for cavity excavation is primarily determined by their size and the degree and pattern of decay present in the main stem or major branches of trees (Bull and others 1997). However, patterns of use may differ among cavity nester guilds and over time. Cavity nesters are typically grouped as strong excavators (i.e., woodpeckers) and weak excavators (i.e., nuthatches and chickadees)—both of which groups excavate their own cavities—and secondary cavity nesters (e.g., squirrels, bluebirds, swallows, and tree-nesting ducks and owls), which use cavities created by woodpeckers, broken branches, or wood decay processes (McClelland and others 1979, Newton 1994). Trees with cavities are often used repeatedly over time, either by the same breeding pair, by different pairs of the same species, or by multiple species either sequentially or simultaneously (Daily and others 1993, Loeb 1993, Sedgwick 1997). The dependence of secondary cavity nesters on the excavations of primary cavity nesters has been well established (Machmer and Steeger 1995).

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Numerous studies have examined attributes of trees preferred by various cavity nesters (Bate 1995, Bull and others 1997, Harestad and Keisker 1989, Raphael and White 1984, Sedgwick and Knopf 1990, Steeger and Hitchcock 1998). Because nest-site availability can be dramatically altered by forest-cutting regimes (Zarnowitz and Manuwal 1985), active nest trees with potential for reuse are among the most important wildlife habitat components that require retention in forestry operations. There is, however, general lack of information on the longevity and repeated use of nest trees.

In this paper, we report on cavity nesters and their choice of nest tree characteristics (i.e., tree species, condition, and size), rates of complete loss or partial breakage of nest trees, and reuse of nest trees by breeding cavity nesters in coniferous forests of southern British Columbia, Canada. Our primary objectives are to examine condition and use of cavity nest trees over time and provide management recommendations for nest-tree retention in operational forestry.

Study Area

We conducted surveys for breeding cavity nesters in the 9,000-hectare Deer Creek watershed of Arrow Forest District, in the Columbia River basin of southern British Columbia (49°30’N, 118°00’W). Elevation of the area surveyed ranges from 500 to 1,450 meters, and the area is generally southwest-facing. Most of the stands surveyed are managed stands of mature forest (85 to 95 years). Dominant conifer species are Douglas-fir *(Pseudotsuga menziesii),* lodgepole pine *(Pinus contorta),* and western larch *(Larix occidentalis),* with a minor component of localized western redcedar *(Thuja plicata),* western hemlock *(Tsuga heterophylla),* western white pine *(P. monticola),* and ponderosa pine *(P. ponderosa).* The minor hardwood component is dominated by trembling aspen *(Populus tremuloides)* and paper birch *(Betula papyrifera).* The most significant forest insects and pathogens include endemic populations of mountain pine beetle *(Dendroctonus ponderosae),* root disease *(Armillaria ostoyae),* and larch dwarf mistletoe *(Arceuthobium laricis).* Based on visible fungal fruiting bodies, common heart-rot fungi responsible for the wood decay that facilitates cavity excavation by primary cavity nesters include white spongy trunk rot *(Fomes fomentarius),* hardwood trunk rot *(Phellinus igniarius)* and aspen trunk rot *(Phellinus tremulae)* on broad-leafed tree species, and red ring rot *(Phellinus pini)* and brown crumbly rot *(Fomitopsis pinicola)* on conifers. Snag densities varied throughout the study area. Some managed stands contained hardly any snags (less than 1 snag per hectare), whereas other stands contained low to moderate densities (10 to 50 snags per hectare). Unmanaged stands with relatively high levels of *Armillaria* root disease contained high densities of snags (greater than 100 snags of 10 cm diameter at breast height or more per hectare; Steeger and Machmer 1995).

Methods

Nest Searching

We conducted nest searches in approximately 50 percent (4,500 hectare) of the Deer Creek watershed, primarily in areas where road access facilitated ground surveys. We searched for active nests of cavity nesters between May and early July 1996 to 1999 by inspecting trees for cavities, examining the ground for fresh wood chips, following adult birds, and listening for begging chicks. We considered a nest cavity to be active if a bird or mammal was observed incubating eggs or caring for young. Most trees were visited at least twice each breeding season to confirm occupation.

Nest Tree Assessments

For each confirmed active nest tree, we recorded tree species, tree diameter at breast height (dbh) measured with a dbh tape, tree height measured with a clinometer, tree condition (alive, dead, hard or soft snag), and location using a global positioning system device. We also noted presence of broken tops or stems, fungal decay (on the basis of visible conks), old excavated cavities, and identified the species of cavity nester using the tree.

We revisited nest trees at least twice during the survey period (no reassessments were conducted in 1995) to determine current tree condition (i.e., unchanged, uprooted, partially or completely broken). We also examined each tree for evidence of new nesting, visually and by tapping on trees. Most breeding cavity nesters were easily flushed from their cavities by this method, with the exception of red squirrels. Our sample, therefore, may underestimate cavity occupancy by red squirrels.

For data analysis on the choice of nest trees by cavity nesters, we took into account that a subset of nest trees contained more than one nest over the study period. To avoid potential pseudoreplication of individual cavity nesters, we removed additional nests of the same cavity-nesting species from the nest tree data set, if individual nest trees were occupied repeatedly by the same species. We performed statistical analyses with JMP statistical software[4] (Sall and Lehman 1996). With respect to the descriptions of nest trees, our study reports on use but not on availability of nest trees; hence, no inference about preference for certain trees can be made.

Results

Cavity Nesters and Their Nest Trees

From 1994 to 1999, we found seven woodpecker, four weak excavators, and five secondary cavity-nesting species *(table 1)* occupying a total of 602 active nests. The proportional distribution of woodpeckers, weak excavators, and secondary cavity nesters in our sample was 59, 26, and 15 percent, respectively. The sample was dominated by 207 red-naped sapsucker and 117 red-breasted nuthatch nests, which together comprised about 54 percent of the sample.

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Table 1—*Tree species used by cavity nesters for breeding in the Deer Creek watershed, southern British Columbia, 1994-1999*[1].

		Tree species[2]							
Wildlife species	**n**[3]	**Tr As**	**Pa Bi**	**We La**	**Do Fi**	**Lo Pi**	**Po Pi**	**WR Ce**	**WW Pi**
Woodpeckers:	263	47	24	14	7	4	4	0.4	0
Red-naped sapsucker *Sphyrapicus nuchalis*	138	51	38	4	7	0	1	0	0
Hairy woodpecker *Picoides villosus*	46	52	20	28	0	0	0	0	0
Northern flicker *Colaptes auratus*	36	50	8	19	11	0	11	0	0
Three-toed woodpecker *Picoides tridactylus*	23	9	0	30	9	43	4	4	0
Pileated woodpecker *Dryocopus pileatus*	11	73	0	0	0	0	27	0	0
Black-backed woodpecker *Picoides arcticus*	6	0	0	66	33	0	0	0	0
Downy woodpecker *Picoides pubescens*	3	66	0	0	33	0	0	0	0
Weak excavators:	148	17	21	15	42	3	2	0.7	0
Red-breasted nuthatch *Sitta canadensis*	110	7	19	15	54	2	3	0	0
Blacked-capped chickadee *Poecile atricapillus*	15	33	53	0	13	0	0	0	0
Mountain chickadee *Poecile gambeli*	12	50	8	33	0	8	0	0	0
Chestnut-backed chickadee *Poecile rufescens*	11	55	9	9	9	9	0	9	0
Secondary cavity nesters:	84	17	25	36	4	12	2	2	2
Northern flying squirrel *Glaucomys sabrinus*	45	29	33	22	4	9	0	2	0
Red squirrel *Tamiasciurus hudsonicus*	19	0	32	47	5	11	0	5	0
Brown creeper *Certhia americanus*	18	0	0	56	0	22	11	0	11
All species combined	495	33	23	18	17	5	3	0.8	0.4

[1] Numbers are percent of each sample (n = number of nest trees).

[2] TrAs = trembling aspen, PaBi = paper birch, WeLa = western larch, DoFi = Douglas-fir, LoPi = lodgepole pine, PoPi = ponderosa pine, WRCe = western redcedar, WWPi = western white pine.

[3] American kestrel *(Falco sparverius)* and Common goldeneye *(Bucephala clangula)* had a sample size of 1 and were in a trembling aspen and western larch, respectively.

Nest Tree Species

A total of 420 nest trees (containing 602 nests) were occupied by cavity nesters over the six breeding seasons. Some trees contained more than one nest, concurrently or in different years, and of the same or a different cavity-nesting species. Discounting 107 potentially pseudoreplicated nests, a total of 495 nests of different species were observed in the 420 nest trees. Eight tree species were used for nesting *(table 1)* of which, in order of most frequent use, trembling aspen, paper birch, western larch, and Douglas-fir accounted for most (91 percent) nest trees. Use of the four most-commonly used tree species by cavity-nesting guilds was significantly different from expected frequencies (chi-square = 134; d.f. = 6; $p < 0.0001$; *table 1*). In addition, pair-wise comparisons between guilds indicated different use patterns of tree species ($p < 0.001$ for all three comparisons). However, some similarities existed: woodpeckers and the secondary cavity-nesting guild (especially squirrels that use woodpecker cavities) primarily nested in aspen, birch and larch, whereas weak excavators most often used Douglas-fir. Aspen was used more often for nesting than any other tree species by five of the seven woodpecker species. A total of 75 percent of the 16 cavity-nesting species used aspen at least once.

The three-toed woodpecker used mostly coniferous species, especially larch and lodgepole pine (30 and 43 percent, respectively). Douglas-fir was very important to one species in particular, the red-breasted nuthatch, accounting for 54 percent of its nests. All cavity-nesting species with a nest sample greater than two used more than one tree species for nesting. The pileated and black-backed woodpeckers appeared to be selective in our study area with respect to tree species, using only two species: aspen and ponderosa pine and larch and Douglas-fir, respectively. Four cavity-nesting species showed considerable flexibility with respect to the species of tree they chose to nest in: three-toed woodpecker, red-breasted nuthatch, chestnut-backed chickadee, and northern flying squirrel each used six different tree species.

Nest Tree Condition

With the exception of aspen, most nest trees of all species (particularly ponderosa pine and Douglas-fir) were dead at the time of first detection *(fig. 1)*. Dead nest trees were predominantly classified as hard snags, except for Douglas-fir, most of which were classified as soft snags *(fig. 1)*. A high proportion of Douglas-fir, ponderosa pine and birch were partially broken and a high proportion of birch had visible evidence of wood decay (i.e., conks) *(fig. 1)*.

More than half (55 percent) of 495 nest trees located in this study were dead when first recorded with an active nest *(table 2)*. Selection of dead trees for nesting differed among the three guilds (chi-square = 55.5; d.f. = 2; $p < 0.0001$). Woodpeckers used living trees more than dead trees, whereas weak excavators used primarily dead trees and did so more than did secondary cavity nesters (Fisher's exact 2-tailed test; d.f. = 1; $p = 0.06$). The trend for woodpeckers to use living trees for nesting, however, is largely a result of their extensive use of living aspen. Removing aspen from this analysis shows that the majority of woodpecker nests (63 percent of 139 nests) were also located in dead trees. The proportional use of dead trees by individual cavity nesters (with sample size greater than 5) ranged from 33 – 50 percent in woodpeckers, 18 – 89 percent in weak excavators, and 51 – 94 percent in secondary cavity nesters. Almost all brown creeper nests found were in dead trees and constructed behind loose bark rather than in cavities in the stem or major branches of trees.

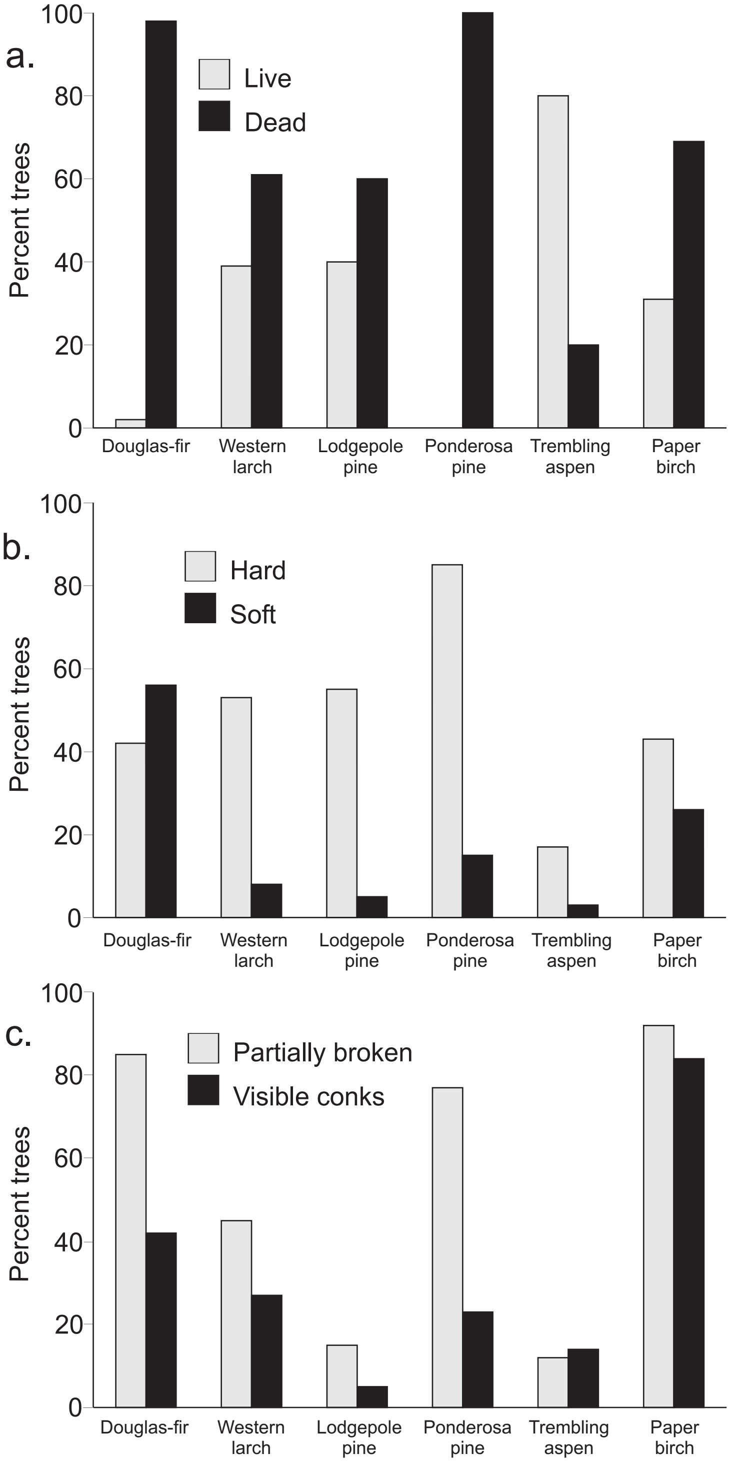

Figure 1—Proportion of nest trees that were (a) either living or dead, (b) dead with hard or soft stemwood, and (c) partially broken (> 2 meters standing) and/or showing visible sign of fungal decay (conks) in the Deer Creek watershed, southern British Columbia.

Table 2—*Proportion of nest trees that were dead when used by cavity nesters in the Deer Creek watershed, southern British Columbia, 1994-1999.*

Wildlife species	n[1]	Percent dead nest trees
Woodpeckers:	263	40
Red-naped sapsucker	138	41
Hairy woodpecker	46	33
Northern flicker	36	36
Three-toed woodpecker	23	48
Pileated woodpecker	11	36
Black-backed woodpecker	6	50
Downy woodpecker	3	67
Weak excavators:	148	76
Red-breasted nuthatch	110	89
Blacked-capped chickadee	15	60
Mountain chickadee	12	33
Chestnut-backed chickadee	11	18
Secondary cavity nesters:	84	4
Northern flying squirrel	45	51
Red squirrel	19	68
Brown creeper	18	94
All species combined	495	55

[1] American kestrel and Common goldeneye had a sample size of 1 and were in a live and dead tree, respectively.

Nest Tree Size

Comparison of the six tree species that contained more than one percent of active *(table 1)* showed that the interquartile range of diameter values increased with increase in median, with ponderosa and lodgepole pine showing the widest and narrowest range, respectively *(fig. 2)*. Mean diameters of nest trees differed significantly among the conifers ($F_{3,185}$ = 14.1; $p < 0.0001$); however, post-hoc comparison of means between the two most commonly-used conifer species, Douglas-fir and western larch, indicated no significant difference (Tukey Kramer test $\alpha = 0.05$). The two species of broad-leafed nest trees, trembling aspen and paper birch, also differed significantly in mean diameter ($t_{1,223}$ = 4.6; p $p < 0.0001$), and were, on average, smaller in diameter than the coniferous nest trees ($t_{1,412}$ = 6.2; $p < 0.0001$). Douglas-fir nest trees showed the second largest mean diameter, despite being used primarily by small-sized, weak excavators *(table 1)*. For all tree species, 90 percent of all nest trees were larger than 18.5 cm in diameter.

Comparison of the three cavity nester guilds showed similar patterns of the range of diameter values around the median *(fig. 2)*, especially between woodpeckers and secondary cavity nesters. Mean diameters of nest trees did not differ significantly ($F_{2,418}$ = 1.08; $p = 0.34$) among the three guilds of cavity nester. Ninety percent of nest trees used by woodpeckers and secondary cavity nesters were larger than 23.1 cm in diameter, while 90 percent of nest trees used by weak excavators were larger than 16.4 cm in diameter.

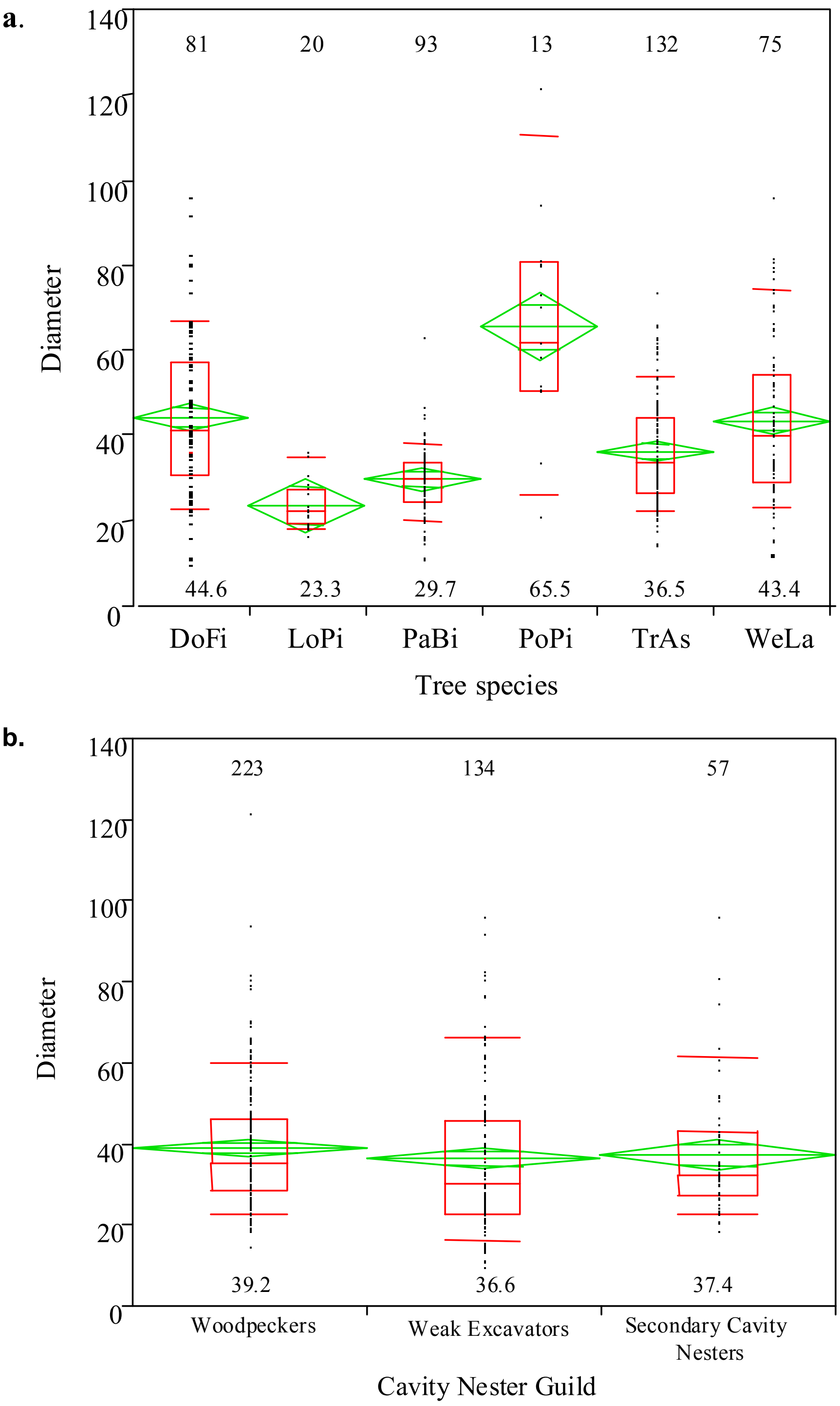

Figure 2—Central tendencies and associated variations in diameter (cm) values of nest trees by tree species (a) and cavity nester guild (b), Deer Creek watershed, southern British Columbia. Shown are distribution of all points, quantile box plots with medians, interquartile ranges (boxes) and 10 percent and 90 percent quantile lines, and means diamonds with means (center lines) and 95 percent confidence intervals (top and bottom of the diamonds). Sample sizes and mean values are given at the top and bottom of the panels, respectively.

Nest Tree Dynamics

Changes in Nest Tree Conditions

We considered all trees with active nests located within one season as a "nest-tree cohort" *(table 3)*. Over time, trees within a cohort either changed condition (e.g., they partially broke) or they were completely lost due to total breakage, uprooting, or forestry operations (i.e., tree cutting or road building). Over the study period, the average annual rate of nest tree loss due to natural causes (range: 3.0 to 4.5 percent/year, *table 3*) was fairly constant for each cohort, although there were differences in rates between the causes of tree loss. The annual proportion of nest tree loss due to natural causes for individual years (n = 15 for the five cohorts) ranged from 1.5 to 6.1 percent (data not shown). Average annual rates of partial tree breakage were generally similar to those for complete losses. We also report annual rates of nest tree loss due to forestry operations for comparative purposes, although these values are based on forest management decisions and vary accordingly. For the oldest nest-tree cohort (1994), we observed a total reduction in available nest trees of 48.5 percent over the 5-year period *(fig. 3)*.

Table 3—*Changes in nest-tree cohorts found annually from 1994-98; numbers are average (except for the 1998 cohort) annual rates of change (in percentages) of the original samples.*

	Nest-tree cohorts (initial number of trees)				
	1994 (66)	**1995 (99)**	**1996 (70)**	**1997 (64)**	**1998 (89)**
Tree loss due to natural causes: [1]	3.0	3.0	3.8	3.1	4.5
Trees partially broken (> 2 meters standing)	5.1	6.5	2.8	3.1	1.1
Tree loss directly due to forestry operations	6.7	3.3	0.9	1.6	2.3

[1] Causes included total breakage (< 2 m standing) or uprooting. Note that uprooting of some trees may have been indirectly caused by forestry operation via windthrow along the margins of cutblocks or roads.

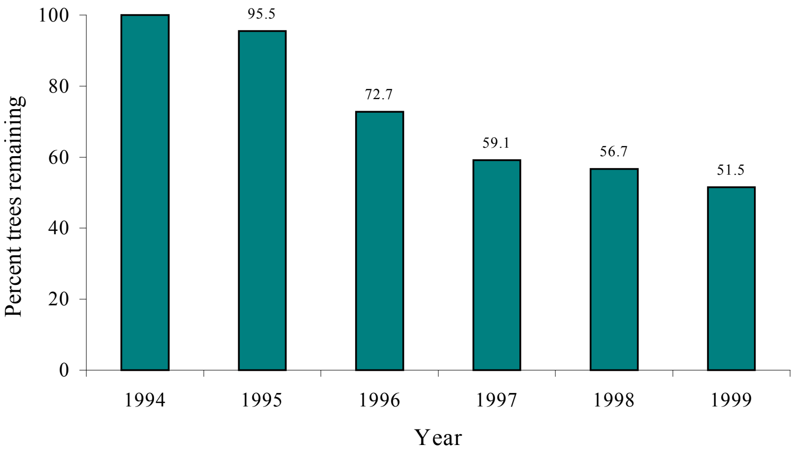

Figure 3—Reduction of the 1994 nest tree cohort (initial n = 66 nests) over 5 years in the Deer Creek watershed, southern British Columbia. Partially broken trees (> 2 meters standing) are included.

Reuse of Nest Trees

All tree species showed multiple excavated (nest or roost) cavities in individual trees, but there was a wide range of variation in the average and maximum number of cavities among species *(table 4)*.

Table 4—*Number of excavated cavities in individual trees, by tree species, in the Deer Creek watershed, southern British Columbia, 1994-1999.*

Species	n	Mean # of cavities (s.e., range)
Trembling aspen	132	3.6 (0.3, 1-14)
Ponderosa pine	13	3.4 (1.0, 1-11)
Paper birch	93	2.9 (0.3, 1-14)
Western larch	75	2.5 (0.3, 1-14)
Douglas-fir	81	2.0 (0.1, 1-7)
Lodgepole pine	20	1.2 (0.2, 1-4)

Reuse of nest trees involving new cavity excavation is generally higher in broadleafed trees compared to conifers, primarily due to the woodpeckers' (especially red-naped sapsucker) frequent use of living aspen *(table 1, fig. 1)*. Among conifers, ponderosa pine and larch showed relatively high mean, maximum and variation in number of cavities. Lodgepole pine had the lowest mean, maximum and variation in number of cavities *(table 4)*; we only detected three-toed woodpeckers and the occasional weak excavator constructing nest cavities in lodgepole pine *(table 1)*. Overall, we detected multiple excavated cavities in 55.5 percent of all nest trees (n = 420), with larger trees containing more cavities than smaller trees ($r = 0.13$, $P < 0.01$). The proportion of trees with different numbers of multiple cavities was:

Number of cavities	Percent of nest trees
2	18.6
3	11.2
4	7.9
5	4.8
6	5.7
7-14	7.4

During the study period, 30 percent of all available nest trees (n = 385) were reused, by the same and/or one or more different species in at least one subsequent year. Reuse by the same, one or two different species occurred in 19, 14, and 2 percent of nest trees, respectively. We observed two simultaneously active cavity nests in 4 percent of all nest trees (n = 420), always by two different cavity-nesting species. The frequency of reuse of nest trees (maximum = five times) and the proportion of trees in each category was: once = 21 percent, twice = 5 percent, three times = 2 percent, four times = 0.8 percent and five times = 0.3 percent.

Discussion

Cavity nesters detected within our study area used a total of eight tree species for breeding sites, with variation in the pattern of use among the different cavity-nesting species and guilds. Based on the tree species used and the condition of nest trees, woodpeckers primarily used living trees (e.g., aspen) and hard snags (e.g., larch and lodgepole pine) for nesting. The pileated and black-backed woodpeckers were found in only two tree species which is consistent with the results of an extensive woodpecker study by Bull (1980). Our sample sizes for these species are low, however, and both species have been reported breeding in tree species different from the species reported in this study (Bull 1980, Raphael and White 1984). We found weak excavators nesting mostly in dead trees with advanced decay (e.g., Douglas-fir killed by *Armillaria* root disease and infected by *Phellinus pini*) and in partially broken trees. Red-breasted nuthatches, for example, most often nested near the break of broken-top trees (Steeger and Hitchock 1998). Eighty-five percent of 110 nuthatch nest trees located in the present study were partially broken. While we recorded presence of visible conks on nest trees, many living trees did not show any sign of fungal wood decay. However, because they were excavated by primary cavity nesters, they likely contained some wood decay at the level of the nest cavities (Conner and Locke 1982, Parks and others 1996). Most nest trees in our study were dead.

Ponderosa and lodgepole pine nest trees showed the highest (65.5 cm) and lowest (23.3 cm) mean diameter, respectively. We do not have information on the proportions of different tree species and their diameter distributions in the study area and therefore cannot address preference for certain species and diameters by breeding cavity nesters. However, preference for large-diameter snags has been well documented for a variety of cavity nesters (see references in Bull and others 1997). In our study, mean diameter of all nest trees was 38.1 cm. Mean diameter of nest trees of woodpeckers, weak excavators, and secondary cavity nesters was 39.2 cm, 36.7 cm, and 37.1 cm, respectively. These mean diameter (dbh) values are notably lower than those reported for cavity nest trees by, for example, Mannan and others (1980; greater 60 cm in western Oregon), Raphael and White (1984; 62.3 cm in northern California), and Lundquist and Mariani (1991; 75.8 cm in southern Washington) but are similar to those reported by Harestad and Keisker (1989; 32.3 cm in southcentral British Columbia). This difference in mean nest tree diameter between these United States and British Columbia studies may be related to the tree species and their diameter distribution available for cavity nesting in the respective study areas. However, regardless of the reason for this difference, our study shows that trees less than 40 cm in diameter are frequently used for cavity nesting, but we do not know the reproductive success of the breeding pairs we observed. A valuable contribution by further studies on cavity nest trees would be to examine reproductive success of pairs breeding in trees within a range of different characteristics.

Average annual nest tree losses due to natural breakage or uprooting (i.e., not directly caused by tree cutting) ranged from 3.0 to 4.5 percent. These values are higher than the average annual 1.7 and 1.1 percent reported for attrition of pileated woodpecker nest trees by Bull (1987) and Bonar (2000), respectively. Our sample included nest trees of 16 cavity-nesting species, some of which are weak excavators that generally breed in dead and more decayed trees with presumably higher fall rates than those reported by Bull (1987) and Bonar (2000). The fall rates in our study are lower than those reported by McCelland (1977) who observed for seven cavity nesters a loss of 9 out of 83 nest trees over 2 years (or 5.4 percent annually), but at least two of his nine trees were cut. The average annual rates of nest tree losses documented in our study are based on annual cohorts of all nest trees sampled. Therefore, the rates primarily represent nest tree loss of the most common nest tree species (i.e., aspen, birch, Douglas-fir, and larch) together. Rates of individual species may differ and will be evaluated when sample sizes are sufficient.

Most nest trees (55.5 percent) in this study showed evidence of multiple cavity excavation. The number of multiple cavities in some trees may be underestimated as trees that were partially broken when first detected may have had other cavities in the part of the trunk that had broken off. Also, because more than half of all nest trees already contained two or more excavated cavities when first detected, our values for reuse of nest trees are potentially underestimates and some cavities may have gone undetected. Multiple nest cavities in trees have previously been documented by Sedgwick and Knopf (1986), who found 38.5 percent of all cavity trees had multiple excavations and that, consistent with our results, larger trees had more cavities than smaller trees. The observed multiple use of large-sized trees by cavity nesters, either sequentially over several years or simultaneously, indicates the high habitat and conservation value of such trees.

Management Implications

The low-elevation coniferous forests of the southern interior of British Columbia are characterized by a high diversity of tree species (Meidinger and Pojar 1991) that supports a variety of primary and secondary cavity nesters. Seven sympatric woodpecker species occur in our study area, which is near the maximum number reported for North America (Short and Horne 1990). Because woodpeckers and other cavity nesters play important ecological roles in forest ecosystems (e.g., regulation of insect populations, [Machmer and Steeger 1995], keystone cavity excavators in nest webs [Martin and Eadie 1999]) and are potentially negatively affected by intensive forestry, preservation of their nest trees has become part of forest management in British Columbia.

Although some tree species such as aspen and larch are used by a variety of cavity nesters, other tree species are used by only a few individual cavity nesters (e.g., use of lodgepole pine by three-toed woodpeckers). Retention of nest trees during forestry and other land-use operations, therefore, may be most beneficial to the diversity of cavity nesters if sets of tree species are retained that are representative of the pre-harvest stand composition. Of particular importance for any retention strategy are broad-leafed trees with evidence of nest cavities, especially in stands in which these species constitute a minor component of the tree species composition. Large-diameter ponderosa pine snags are important nest trees for woodpeckers potentially over long periods of time, as indicated by the high number of nest cavities they contain in our study area; they should be retained wherever possible. In stands with high levels of bark beetle populations, selective harvesting of infested or susceptible pine should include some pine retention to provide current and future nesting as well as foraging opportunities, especially in three-toed woodpecker home ranges.

For cavity nesters in general, dead and partially broken coniferous and broad-leafed trees and trees with fungal wood decay are essential habitat components. Under endemic levels of natural disturbance agents (insects and diseases) and in the absence of catastrophic winds and fires, the annual rate of nest tree loss due to natural causes is less than 5 percent in our study area and may be in balance with new trees becoming suitable for cavity nesting. However, forestry operations such as road building and logging along with unregulated firewood cutting can lead to dramatic reductions in habitat for cavity nesters over extensive areas of the landscape. Because primary cavity nesters are territorial during the breeding season (i.e., they exclude conspecifics from a given area), establishment of zones where intensive forestry is practiced without retention of dead and diseased trees will lead to declines in cavity nester populations, as these zones will not be able to contain more breeding pairs as set by the species' territory size requirements. Cavity nester populations fluctuate naturally in any given area according to the often ephemeral availability of essential resources such as nest sites and feeding opportunities (Baldwin 1968, Otvos 1979). However, elimination of dead and diseased trees that provide habitat for cavity nesters is a systematic and, to some extent, inevitable process in industrial forestry that most probably effects the natural dynamics of populations. If intensive forestry zones are too wide-spread, species of cavity nesters may become endangered or locally extirpated as, for example, in the managed taiga forests of Sweden that are suffering severe losses of broad-leafed and dead trees (Angelstam 1990, Angelstam and Mikusinski 1994). In British Columbia, the Wildlife/Danger Tree Assessor's Course and the recently revised occupational health and safety regulations of the Workers' Compensation Board now allow for retention of dead trees in all forestry operations, provided they do not pose a hazard to forest workers (Manning and others 2002). Successful implementation of these new initiatives will be an important step in conserving the habitat of cavity nesters in British Columbia.

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How Dead Trees Sustain Live Organisms in Western Forests[1]

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Abstract

Dead wood contributes to biological richness as substrate, cavity sites, foraging sites, and shelter or cover. In the Pacific Northwest, 69 vertebrate species commonly use cavities, 47 species respond positively to down wood, and prevalence of both uses is related to natural fire regimes. Almost 80 percent of nests of weak excavators are in dead trees; strong excavators make greater use of live trees. Most bat roosts are in dead trees, whereas carnivores use mostly declining, living trees. Selection of both cavity and foraging sites is governed by decay patterns. Some species prefer large pieces of down wood. Management implications are discussed.

Introduction

Dying trees, snags, and down wood are common in unmanaged forests and required by many species, including fungi, cryptogams, invertebrates, and vertebrates (Berg and others 1994, Harmon and others 1986). We focus on vertebrates, and note contributions to non-vertebrates only briefly. We also focus on the Pacific Northwest, which we define as Alaska, Alberta, British Columbia, Washington, Oregon, Idaho, Montana, and northern Nevada and California. References to other regions are included to indicate trends where forestry has been practiced longer, or where particular species are well documented.

As concern for sustaining all organisms has grown, interest in natural disturbance regimes as models for guiding forest practices has also increased (Attiwill 1994, Hunter 1993). We first examine relations among natural fire regimes and vertebrates that use dead wood. We then review the diverse uses forest-dwelling organisms make of dead wood under four broad categories: substrate, cavity sites, foraging sites, and shelter or cover (down wood). We finish by noting management implications.

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Natural Disturbance Regimes and Use of Dead Wood

Fire is the major natural agent of disturbance in Pacific Northwest forests, and natural fire regimes differ among forest types, influencing the amounts of dead wood present (Agee 1993). We examined relationships of the forest-dwelling vertebrate fauna with natural fire regimes in the 12 forested biogeoclimatic zones of British Columbia, applying the approach of Bunnell (1995) to more recent data. We expected predictable differences. The proportion of species positively associated with down wood should increase as the fire-return interval increased and down wood accumulated. Cavity users should be negatively correlated with fire size, because size and intensity often are related, and fewer snags remain standing where fires are more intense.

The proportion of down wood users in the fauna increased with increasing fire-return interval, and proportions of bird and mammal cavity users decreased with increasing fire size *(table 1).* Species using down wood are mainly mammals *(appendix A),* and both numbers of species and proportions of mammalian users of down wood increased with increasing fire size. That is expected if larger, more intense fires create a more reliable supply of down wood. The number of species using cavity sites decreased significantly as fire return interval lengthened, and snags were created less frequently *(table 1).* Fire regimes vary with the precipitation regime, but associations between the vertebrate fauna and precipitation regimes were not found. The lack of relations with total precipitation suggests that fire regime had more influence on composition of the vertebrate fauna than precipitation itself (the two wettest types were also higher elevation and obscured any relationship between amphibian richness and precipitation).

Forest-dwelling vertebrate faunas appear to respond to amounts and duration of down wood as these are influenced by the natural disturbance regime, suggesting a mechanism for the differences in richness of dead wood users across broad forest types.

Table 1—*Significant Spearman's rank coefficients among vertebrates using dead wood and mean annual precipitation, and characteristics of natural fire regimes in the 12 forested biogeoclimatic zones of British Columbia.* [1]

	Cavity users						**Downed wood users**			
	All		**Birds**		**Mammals**		**All**		**Mammals**	
	N[2]	Pr[2]	N	Pr	N	Pr	N	Pr	N	Pr
Precipitation								0.59*		
Fire Size		- 0.85**		- 0.75**		- 0.70*			0.66*	0.68*
Fire Return	- 0.58*		- 0.79**					0.83**		

[1] * = P < 0.05; ** = P < 0.01

[2] N = Number of species; Pr = Proportion of species in the native vertebrate fauna.

Dying and Dead Wood as Substrate

Dead wood makes its greatest contribution to biological richness as substrate for fungi, cryptogams, and invertebrates. There are no sharp distinctions between declining trees and snags as the most favored habitat. Some pendent lichens are common on both, but appear more abundant on snags (e.g., *Usnea longissima,* Berg and others 1994; *Letharia vulpina,* Bernes 1994). Berg and others (1994) reviewed habitat requirements of 1,487 threatened forest-dwelling organisms in Sweden. Dying trees were favored habitat for 89 species of fungi and cryptogams and 252 species of invertebrates. Snags provided substrate for 21 percent of all threatened non-vertebrate species, including 36 macrofungi and cryptogam species and 266 invertebrates. Logs hosted more species. Berg and others (1994) estimated that about 30 percent of threatened cryptogams and macrofungi and 28 percent of the invertebrates were dependent on down wood.

The role of dead wood as substrate is less well known in the Pacific Northwest, but likely is similar to the role in Sweden. Of 636 lichen species reported from British Columbia 46 are largely restricted to old-growth stands (Goward 1999; Goward and others 1994). Goward and Arsenault (1997) reported a snag-specific community of lichens from Englemann spruce *(Picea englemanni;* scientific names for most species are found in *appendix A)* and subalpine fir *(Abies lasciocarpa)* forests. At least 25 lichen species are found on decaying wood (data in Goward 1999, and Goward and others 1994). Of 93 forest-dwelling bryophytes reviewed by Vitt and others (1988) for the Pacific Northwest, 30 species (32 percent) preferentially grow on down wood that frequently is well rotted. Well-rotted logs also serve as foci for dispersal of mycorrhizal fungi critical to tree productivity (Maser and others 1978). Some "saprophytic" vascular plants (e.g., *Allotropa*, *Hemitomes*) rely upon mycorrhizal fungi that often are found in down wood for delivery of nutrients (Leake 1994). In British Columbia, 526 species of macrofungi are dependent on down wood, including some harvested commercially (Lofroth 1998). Because some vertebrates forage on fungi and insects in down wood, reductions of these food sources may appear higher in the food chain.

Features of logs considered to influence non-vertebrates include tree species, decay state, size, and distribution. Conifer logs are more durable than hardwood logs. Natural successions of cryptogams, fungi, and invertebrates on and in down wood (e.g., McCullough 1948, Söderström 1988) indicate the importance of a range of decay states. Larger logs provide better substrate than smaller logs for bryophytes and lichens, because larger logs last longer, have more surface area, and have higher, steeper sides that discourage ground-dwelling species from invading (Samuelsson and others 1994). Forest-floor bryophytes generally have very limited dispersal ability (Khanna 1964, Söderström 1987), and dispersal is from log to log for epixylic species. For these reasons, Samuelsson and others (1994) argued that logs should be close together, but not gathered into piles. Similarly, several small logs may provide more habitat than a single large log.

Dead wood is a critical substrate for hundreds of non-vertebrate species in the Pacific Northwest. Large, dispersed pieces of a range of decay states are preferred. Sustaining a range of decay requires sustained recruitment of down wood.

Dead Wood as Cavity Sites

Cavity sites are easily studied and hence well-documented. Foraging on snags is a year round activity, is less frequently studied, and less well known. Lack of cavity nesting sites has limited abundance of some birds in intensively managed forests (Angelstam and Mikusinski 1994, Newton 1994).

Because of the importance of heart rot for cavity sites, most nests of primary cavity nesters were in dead trees *(table 2).* Of 2,674 nesting records of weak excavators, 2,154 (78 percent) were in dead trees *(table 2)*. Although conifers are less prone to decay than most hardwoods, the proportion of dead trees used as nest sites by weak excavators did not change with the proportion of conifers used. Most strong excavators located < 50 percent of their nests in dead trees *(table 2),* but the proportion of nests in dead trees increased significantly with the proportion of conifers used (Bunnell and others 2002). That relationship explains apparently anomalous values in *table 2*. For example, in the largest sample for pileated woodpecker in *table 2* (Bull 1987; n = 105 nests) all available nest trees were conifers, and 99 percent of the nests were in dead trees. Conversely, another sample was gathered[4] where hardwoods were available but scarce (< 10 percent of stems), but six of seven nest trees were living trembling aspen *(Populus tremuloides)*. Dead trees were the main source of cavity sites for 16 of the 21 primary excavators *(table 2)*. For most of the remaining species, dead trees were more commonly used as cavity sites when nests were in conifers. Weaker excavators largely restricted to conifers (e.g., Lewis's woodpecker, white-headed woodpecker) may be particularly threatened in managed, conifer forests, because trees do not become old enough for heart rots to develop. Both Lewis's and white-headed woodpeckers are designated 'at risk' in the Pacific Northwest *(appendix A).*

Table 2—*Percentages of nests located in dead trees by strong and weak excavators of the Pacific Northwest.*

	Pct dead	n[1]	Sources
Strong Excavators			
Yellow-bellied sapsucker	41.4	63	Scott and others 1980; BC Nest Records.
Red-naped sapsucker	24.0	557	Campbell and others 1990; Li and Martin 1991; C. Steeger[2]; W. Klenner and D. Huggard[3]; K. Martin[4]
Red-breasted sapsucker	55.3	132	Raphael and White 1984; Campbell and others 1990; Li and Martin 1991.
Williamson's sapsucker	59.3	303	Bull 1980; Scott and others 1980; Raphael and White 1984; Li and Martin 1991; Conway and Martin 1993; BC Nest Records.
Hairy woodpecker	62.4	190	Kelleher 1963; Bull 1980; Scott and others 1980; Raphael and White 1984; Campbell and others 1990; Li and Martin 1991; W. Klenner and D. Huggard[3]; K. Martin[4]; C. Steeger[2]
Three-toed woodpecker	42.9	161	Scott and others 1980; Klenner and Huggard 1997; C. Steeger[2]; K. Martin[4]; BC Nest Records.
Black-backed woodpecker	46.7	56	Bull 1980; Raphael and White 1984; C. Steeger (unpublished)[2]; BC Nest Records.
Acorn woodpecker	7.8	238	Scott and others 1980; Li and Martin 1991; Hooge and others 1999.
Pileated woodpecker	73.2	202	Bull 1987; Mellen 1987; Campbell and others 1990; C. Steeger [2]; W. Klenner and D. Huggard[3]; K. Martin[4]; K. Aubry and C. Raley [5]

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[4] Unpublished data on file, British Columbia Ministry of Forests, Kamloops, British Columbia.

(*table 2* continued)

	Pct dead	n[1]	Sources
Weak Excavators			
Lewis's woodpecker	62.4	367	Raphael and White 1984; BC Nest Records
Downy woodpecker	60.4	109	Scott and others 1980; Campbell and others 1990; Li and Martin 1991; C. Steeger[2]; K. Martin[4]
White-headed woodpecker	97.4	123	Raphael and White 1984; Milne and Hejl 1989; Dixon 1995a; Dixon 1995b.
Northern flicker	55.9	717	Bull 1980; Scott and others 1980; Raphael and White 1984; Campbell and others 1990; Li and Martin 1991; W. Klenner and D. Huggard[3]; K. Martin[4]; C. Steeger[2]
Nuttall's woodpecker	94.0	48	Miller and Bock 1972 (review within).
Black-capped chickadee	59.3	17	C. Steeger[2]; K. Martin[4]
Mountain chickadee	65.8	433	Scott and others 1980; Raphael and White 1984; W. Klenner and D. Huggard[3]; K. Martin[4]; BC Nest Records.
Boreal chickadee	87.3	31	Peck and James 1987; Campbell and others 1997.
Chestnut-backed chickadee	58.0	132	C. Steeger[2]; BC Nest Records.
Red-breasted nuthatch	71.9	394	Raphael and White 1984; W. Klenner and D. Huggard[3]; K. Martin[4]; C. Steeger[2]; BC Nest Records.
White-breasted nuthatch	74.2	62	McEllin 1979; Scott and others 1980; Raphael and White 1984; Li and Martin 1991; Campbell and others 1997.
Pygmy nuthatch	78.0	331	McEllin 1979; Scott and others 1980; Raphael and White 1984; Li and Martin 1991; BC Nest Records.

[1] Number of nest trees.

[2] Unpublished data on file, Pandion Ecological Research, Ltd., Nelson, BC, Canada.

[3] Unpublished data on file, BC Ministry of Forests, Kamloops Region, BC, Canada.

[4] Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

[5] Unpublished data for K. Aubry and C. Raley, sight unseen from Bull and Jackson (1995).

Figure 1 illustrates preferences by woodpeckers for trees in different stages of decay. Decay classes in *figure 1* are those of Thomas and others (1979), and classes 1 and 2 represent healthy and declining, but living, trees. We used the electivity index of Ivlev (1961) to compare within studies, because it is largely symmetrical, ranging from -1.0 at complete avoidance to about +1.0 when all nests are in a particular category. Living conifers were not selected by either woodpeckers or cavity-using mammals (primarily red and flying squirrels). Living trembling aspen trees were used more in proportion to their availability, except by mammals that cannot excavate their own cavities. The most strongly preferred decay classes were recently dead trees (decay classes 3 and 4). Decay classes 4 and 5 of lodgepole pine *(Pinus concorta)* were strongly avoided because they were long dead, understory trees, too small to support cavities.

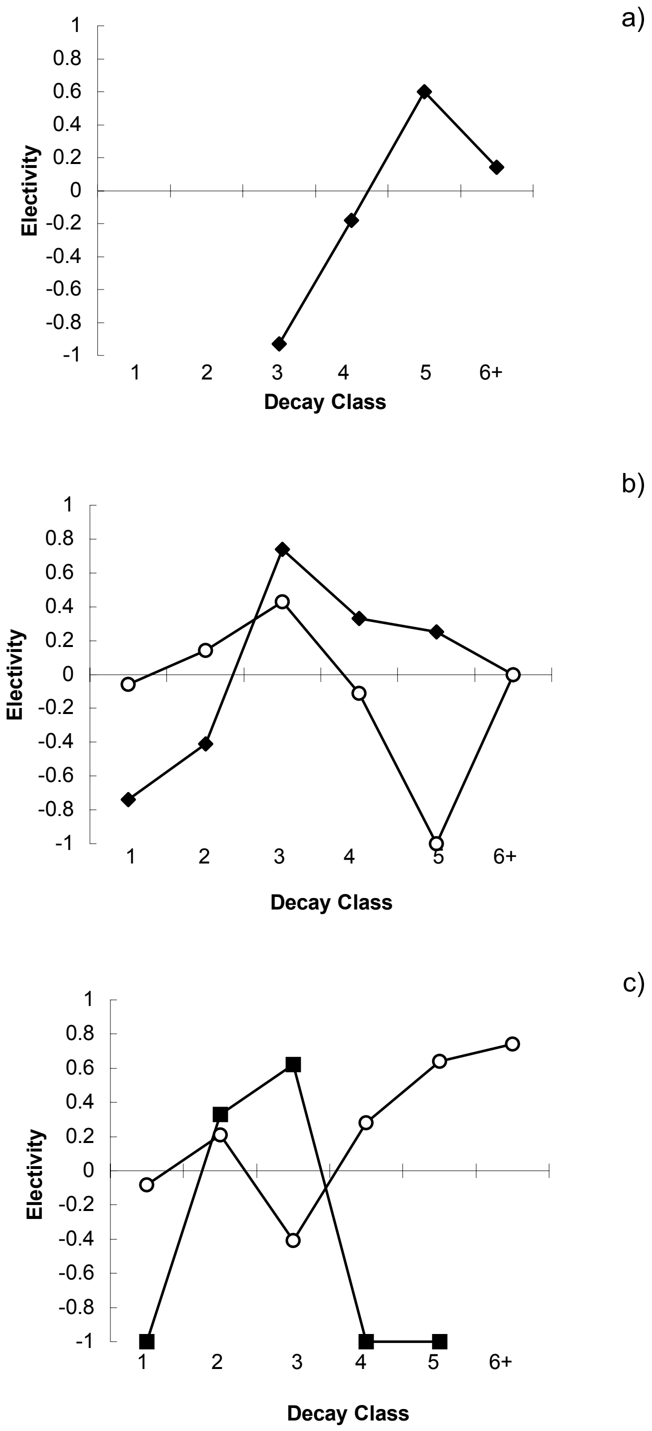

Figure 1—Apparent preference among decay classes shown by: a) woodpeckers nesting in conifers (data of Bevis 1996); b) woodpeckers nesting in Douglas-fir [◆] and trembling aspen trees [O] (data of Klenner and Huggard 1998); c) mammals in lodgepole Pine [■] and trembling aspen trees [O] (data of K. Martin unpublished). Preference evaluated by the electivity index of Ivlev (1961).

There are more secondary than primary cavity nesters *(appendix A),* but often 80 percent or more of their nest sites are created by primary nesters (Dobkin and others 1995, Li and Martin 1991, Schreiber and deCalesta 1992). Other nest sites are in cavities created by rot. For both forms of nest sites, dead trees are the major source of nesting opportunities. Several bat species also locate 70 to 100 percent of their roosts in dead trees *(table 3).* Less than 50 percent of denning trees of flying squirrels, American marten, and black bears were dead, indicating the importance of sustaining older trees with large rot pockets. Most black bear dens recorded from coastal forests of the Pacific Northwest were associated with wooden structures, including trees, logs, and stumps. Den sites in southern, inland forests also were commonly in trees (Bull and others 1996, Lindsay 1999). Mean sizes of den trees for mammals usually exceeded 50 centimeter (references of *table 3*). Amphibians and reptiles make occasional use of cavity sites (McComb and Noble 1981). Bunnell and Dupuis (1995) reported that snags used by amphibians were recently dead with sloughing bark.

Table 3—*Percentage of denning and roosting sites located in snags and dead trees by mammals of the Pacific Northwest. Logs and stumps not included.*

Species	Pct dead	n[1]	Sources
Bats			
Big brown bat	45.8	57	Rasheed and Holroyd 1995; Betts 1996; Vonhof 1996; Kalcounis and Brigham 1998; Rabe and others 1998.
California myotis	100.0	25	Vonhof 1996; Brigham and others 1997; Grindal 1997.
Fringed myotis	100.0	15	Rabe and others 1998.
Little brown myotis	63.2	23	Crampton and Barclay 1995; Rasheed and Holroyd 1995; Kalcounis and Hecker 1996; Grindal 1997.
Long-legged myotis	90.2	54	Rasheed and Holroyd 1995; Ormsbee and McComb 1998; Rabe and others 1998.
Northern long-eared myotis	42.9	7	Caceres 1997.
Pallid bat	100.0	3	Rabe and others 1998.
Silver-haired bat	72.0	50	Crampton and Barclay 1995; Rasheed and Holroyd 1995; Betts 1996; Campbell and others 1996; Vonhof 1996.
Southwestern myotis	0.0	2	Rabe and others 1998.
Western long-eared myotis	89.5	47	Caceres 1997; Grindal 1997; Vonhof and Barclay 1997; Rabe and others 1998.
Rodents			
Flying squirrel	32.1	627	Mowrey and Zasada 1984; Carey and others 1997.
Carnivores			
Black bear	32.1	249	Lindzey and Meslow 1976; Noble and others 1990; Immell and Boulay 1994; Akenson 1994; Bull and others 1996; Davis 1996; Lindsay 1999.
American marten	40.3	470	Spencer 1987; Martin and Barratt 1991; Jones and others 1997; Raphael and Jones 1997; Ruggiero and others 1998.

[1] Number of denning or roosting sites.

Dying and Dead Trees as Foraging Sites

Long-term management of snag-using species requires provision of both foraging and cavity sites. Several studies suggest that cavity sites are less often limiting to cavity nesters than foraging habitat (Hutto 1995, Walankiewicz 1991, Welsh and Capen 1992). Given the relative lack of data for foraging sites, a key question is: are the kinds of trees that should be retained for foraging similar to those that provide nesting sites?

Among larger excavators, sapsuckers feed primarily on sap and insects associated with their sapwells. Northern flickers feed on ants on the ground (Bull and others 1986). Several woodpeckers feed primarily by flaking bark or probing after insect larvae in the cambium or sapwood. Pileated woodpeckers specialize on carpenter ants excavated from decayed sap- or heartwood (Bull and others 1986). For the latter two feeding techniques, decay state may reflect the likelihood of hosting preferred insects and the ease of excavating. It is less clear that size of tree should influence feeding preference, although duration of decay states and size of tree often are correlated. If decay state indicates foraging opportunities, we expect patterns specific to individual tree species, because species decay differently.

Figure 2 shows that conifers were avoided as feeding sites until they attained decay class 3 (recently dead). Their attractiveness as foraging sites then increased with further decay (see also Gyug and Bennett 1996), although that pattern differs among cavity-nesting species (Morrison and others 1987). In Englemann spruce-subalpine fir forests, three-toed woodpeckers strongly preferred recently dead snags (Klenner and Huggard 1997). Pileated woodpeckers use more decayed wood, provided it hosts carpenter ants (Bull and others 1992). Among conifers, Douglas-fir *(Pseudotsuga menzieseii)* is a possible exception *(fig. 2),* and appears to become less attractive to woodpeckers once all bark is shed (decay class 6+). That may reflect Douglas-fir tending to rot from the outside in, so the sapwood becomes less favorable to breeding insects. On Bevis' (1996) study area, Douglas-fir was not sought as a foraging site (electivity = -0.04), and selection was shown only for western larch *(Larix occidentalis)* (electivity = 0.25). Douglas-fir snags also were not selected on Madsen's (1985) study site (electivity = -0.21), whereas western larch and ponderosa pine *(Pinus ponderosa)* were selected (electivity = +0.15 and +0.20, respectively).

Selection of trembling aspen followed a different pattern than for conifers. Foraging woodpeckers were indiscriminate in their use of decay classes 1 through 3 (apparently healthy to recently dead trees), but tended to avoid trees of decay class 4 or greater *(fig. 2).* Woodpeckers tend to use more of the smaller diameter trees when foraging than when nesting, especially when foraging on hardwoods *(fig. 3).*

We draw two broad points from comparisons of nesting and foraging sites. First, when foraging on conifers, woodpeckers select dead wood. The wood need not be standing, and several species forage on down wood when it is not snow covered (Bull and others 1997). Second, woodpeckers will use smaller trees when foraging than when nesting. Birds select similar decay states when foraging or nesting (compare *figs. 1*, *2),* but smaller snags are used when foraging *(fig. 3).* The tendency for nesting trees to be larger than foraging trees makes biological sense: a cavity site must be large enough to contain an adult bird and its young; a foraging site need only be large enough to contain wood-boring larvae or ants. The trend is consistent across studies (e.g., Bevis 1996, Gyug and Bennett 1996). Small snags do not remain standing for as long as large snags (Morrison and Raphael 1993), and may never be used as nest trees. Nonetheless, they do serve as foraging sites.

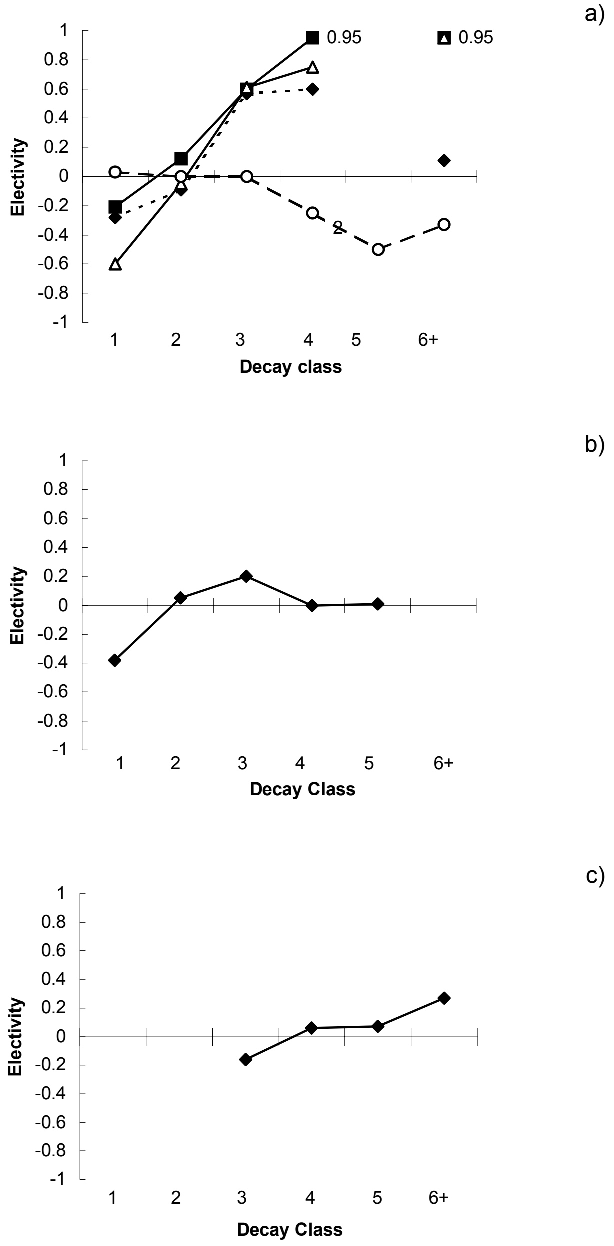

Figure 2—Apparent preference among decay classes shown by foraging cavity nesters. a) Woodpeckers foraging on Douglas-fir [– –◆– –], lodgepole pine [—■—], spruce [—**Δ**—], and trembling aspen trees [– – **O** – –] (from data of Klenner and Huggard 1998). b) Cavity nesting birds foraging on conifers (from data of Madsen 1985). c) Woodpeckers foraging on conifers (from data of Bevis 1996). Values of 0.95 represent instances where specific decay or size classes were sufficiently uncommon that they did not appear in the random sample of availability. Preference evaluated by the electivity index of Ivlev (1961). Decay classes of Thomas and others (1979).

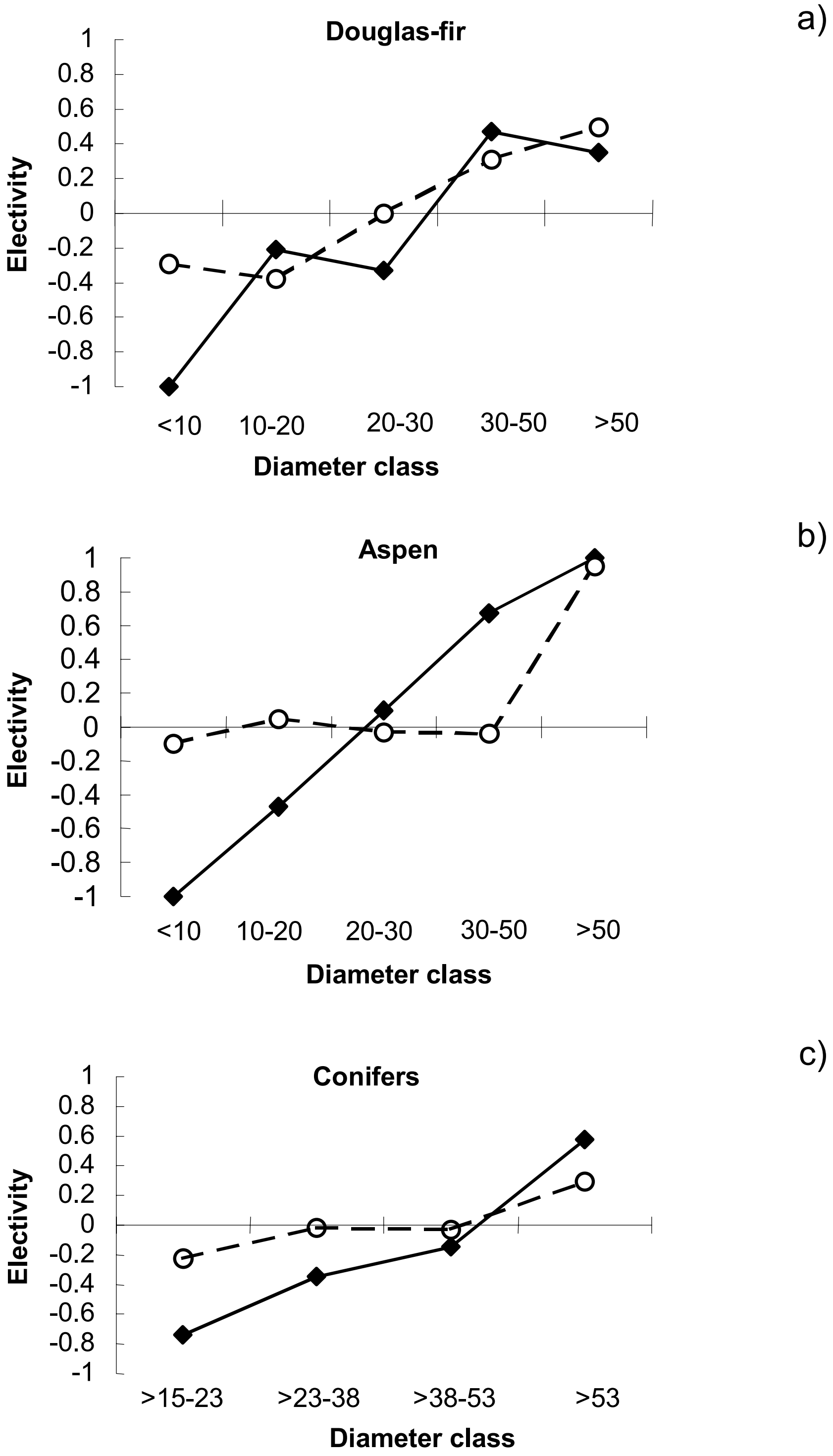

Figure 3—Comparisons of electivity shown by foraging [– – **O** – –] and nesting [—◆—] woodpeckers across diameter classes. Data for a) Douglas-fir from Klenner and Huggard (1998), b) Trembling aspen from Klenner and Huggard (1998), c) Conifers from Madsen (1985).

Some species foraging habitats are particularly difficult to incorporate into forest management. Both the black-backed and three-toed woodpeckers are specialized feeders commonly exploiting conditions after fires (Apfelbaum and Haney 1981, Hutto 1995). Three-toed woodpeckers feed primarily on larvae of bark beetles (Murphy and Lehnhausen 1998) that respond dramatically to forest fires, laying eggs in surviving trees and snags almost immediately after the fire. Adults emerge 2 to 3 years later, and secondary outbreaks appear rare. Although they do eat larvae of wood-boring beetles (Cerambycidae) in other snags, food is most abundant for these woodpeckers for only a 2- to 3-year, post-fire period. Black-backed woodpeckers specialize on larvae of wood-boring beetles that bore into the sapwood of fire- or beetle-killed trees. Populations of both woodpecker species are therefore irruptive and concentrated in areas of beetle-infested trees, and both are listed "at risk"' in the Pacific Northwest *(appendix A).*

Kreisel and Stein (1999) found foraging woodpeckers in winter to be ten times more abundant in recently burned forest than in unburned forest. Hutto (1995) reported that 15 bird species occurred more frequently in burns than any other cover type, including four cavity nesters: hairy, three-toed, and black-backed woodpeckers, and the mountain bluebird. The black-backed woodpecker is the most vulnerable, because of its specialization on wood-boring larvae (rather than bark beetles or free-flying insects). In short, 15 bird species have recent burns as their favored habitat and at least one is dependent upon burns.

The problem for forest management is that beetle-infested stands provide the ideal (and possibly only productive) habitat for some woodpecker species. Numbers of black-backed woodpecker are much lower in older forests than among recent fire-killed trees so that even maintenance of old stands may not be a sufficient management tactic. Both fire suppression and salvage logging work to the detriment of the species. The life history of the black-backed woodpecker illustrates that commitment to maintaining all of biological diversity is also a commitment to sustaining some areas of dying and dead forest.

Dead Wood as Shelter and Cover

Dead wood on the ground influences vertebrate abundance and richness by providing:

- Necessary substrate, energy, and nutrients for many invertebrates and fungi upon which a wide range of amphibian, reptile, bird, and small mammal species depend for forage (e.g., Bull and others 1997, Maser and Trappe 1984; Rhoades 1986).
- Sheltered areas for reproduction in a range of vertebrates from salamanders to black bears, and cover from aerial predators (e.g., Corkran and Thoms 1996, Harestad 1991).
- A modified microclimate (cooler, moister, more stable temperature than surrounding habitat) that is essential to species that cannot tolerate extremes in temperature or humidity (several amphibians; Heatwole 1962).
- Runways for small mammals and display or lookout posts for birds (e.g., Bull and Henjum 1990, Lofroth 1998).

- Increased habitat diversity and aeration in water by forming riffles, small waterfalls, and pools, thereby creating habitat for amphibians and fish which are in turn fed on by other vertebrates.
- Structures exploited by near-aquatic vertebrates as cover, foraging sites, or basking (e.g., river otter *[Lontra Canadensis],* mink, painted turtles *[Chrysemys picta];* Lofroth 1998).
- Access routes for predators, especially under snow cover (e.g., weasels, marten; Corn and Raphael 1992).

Among terrestrial vertebrates, strict dependence on down wood is most likely among species breeding in rotten wood (e.g., some salamanders). Other species, including shrews and several birds, forage on insects that are abundant in down wood and are often more abundant at sites with more down wood (e.g., Craig 1995, Waterhouse and Dawson 1999). Although several bird species opportunistically exploit down wood for nesting sites (e.g., blue grouse *[Dendracapus obscurus]* and ruffed grouse *[Bonasa umbellus],* Townsend's solitaire *[Myadestes townsendi]),* only one bird species relies largely on down wood for nesting opportunities—the winter wren (Waterhouse 1998). Opportunistic use can be high. For example, Campbell and others (1990) reported that 31 percent of blue grouse nests were alongside logs. Several mammal species, ranging from little brown myotis to black bears, use down wood as resting or denning sites, but most show flexibility across substrates. Rodents, snowshoe hare *(Lepus americanus),* gray wolf *(Canis lupus),* and wolverine *(Gulo gulo)* not only use down wood as maternal or resting dens but also use thickets or earth dens. Hagar and others (1995) estimated that 52 species of mammals in Oregon responded positively to greater amounts of dead wood. Among the 52, 40 were associated with logs as cover for themselves or their prey, but it has proven difficult to associate consistent positive responses in population size or fitness with abundance of down wood (Bunnell and Huggard 1999, Bunnell and others 1999b). We acknowledged that flexibility in *appendix A* by including only species for which a positive response appeared likely from current literature. By using that criterion, 12 to 18 percent of terrestrial forest-dwelling vertebrate species respond positively to increasing amounts of down wood in the 12 major forest types of British Columbia (Bunnell and others 1999b).

The strongest responses to down wood are among terrestrial-breeding salamanders (seven of eight salamander species in *appendix A*). Among habitat variables surveyed, down wood is most consistently related to abundance of terrestrial-breeding salamanders (reviews of Bunnell and others 1999b, deMaynadier and Hunter 1995). Some workers reported these salamanders to be associated with large pieces of down wood (Aubry and others 1988, Whitaker and others 1986). Corn and Bury (1991) found that densities of clouded and western redback salamanders were relatively constant per unit volume of down wood regardless of stand age, indicating the benefits of retaining down wood in younger stands. Other authors have documented positive responses of small mammals to down wood (e.g., Carey and Johnson 1995, Corn and others 1988, Gilbert and Allwine 1991), but results are highly variable within species and among locations. Bunnell and others (1999a) offered four reasons for the observed variability in response to down wood, of which the most troubling is that critical lower thresholds have not been reached.

Where forestry has been practiced longer than in the Pacific Northwest, many organisms are threatened by reductions in down wood (e.g., Anglestam 1997, Berg and others 1994). Current evidence suggests that species dependent upon down wood in the Pacific Northwest are surviving on legacies of past practices, not the results of current practices (e.g., Bunnell and others 1997, Spies and others 1988). We believe that if current accumulations are not replenished, down wood accrued under past practices will decline, as will some species.

Management Implications

In the Pacific Northwest, 69 vertebrate species consistently seek cavities in dying or dead trees, and more use such cavities opportunistically. Another 47 or more species respond positively to increasing amounts of down wood *(appendix A).* The 90 species of forest-dwelling vertebrates in the Pacific Northwest listed as "sensitive" or "at risk," include 30 species requiring cavities and 21 species strongly associated with down wood. (A definition of "forest-dwelling" is problematic, and we excluded species such as peregrine falcon *(Falco peregrinus),* Swainson's hawk *(Buteo swaisoni),* and barn owl *(Tyto alba)* whose relationship with forest cover is marginal.) Thus, about 57 percent of listed vertebrate species are reliant upon or strongly associated with dead wood. Many more cryptogams, fungi, and invertebrates are dependent upon dead wood. Where the goal of management is to sustain or restore native biodiversity, forest practices must include ways of sustaining dead wood. Most managed stands have smaller volumes of dead wood than do unmanaged stands (Maser and Trappe 1984, Spies and others 1988). The trend is pronounced where forestry has been practiced longer. Angelstam (1997) reported that dead wood comprised 30-40 percent of the total wood volume in unmanaged stands and declined to about 20 percent after one rotation and to about 1 percent after several rotations of intensive fiber extraction. The trend is consistent with projections of Spies and others (1988) for the Pacific Northwest. Our review suggests that if managers desire to sustain biodiversity they should:

- *Ensure sustained provision of dying and dead wood*—Hundreds of species depend on dying and dead logs and trees. Where the goal is to sustain all of the biological diversity, patchwise retention incorporating all structures is helpful.

- *Retain trees and snags of both hardwoods and favored conifer species (larch, Douglas-fir, ponderosa pine), particularly where hardwood species are not abundant. Avoid creating monocultures of less preferred species, such as lodgepole pine*—Although they are favored nesting sites and provide the only substrate for some bryophytes, we cannot rely solely on more decay-prone hardwoods. The varied needs of forest organisms include well-decayed snags, large hollow snags, and snags with loose slabs of bark. Hardwood species will not accommodate all these needs, nor will any one species of conifer. Because conifers are longer-lived and provide a longer-lasting source of cavities than do hardwoods (Erskine 1977, Harmon and others 1986), they are more likely to sustain snags late into rotations. Conifer snags are required by species foraging on bark beetles and wood-boring beetles, and conifer logs last longer than do hardwood logs.

- *Retain a range of size and age classes of dead wood*—Where safety considerations eliminate older snags at harvest, managers should ensure that snags can develop through the rotation. Although larger diameters usually are selected by vertebrates, smaller snags and logs are used. The desirability of a range of decay classes is well documented for bryophytes, insects, terrestrial breeding salamanders, and birds. Well-decayed snags present greater safety risks and are more easily retained in patches. Unless reserve patches are very large, recruitment of well-decayed snags must occur outside of reserve patches. Snags may never become well decayed if operational guidelines require snag-falling. Either no-work zones are required during subsequent entries, or silvicultural systems that do not require frequent entries should be employed in at least some areas. Well-decayed snags will not develop at all during a rotation if no trees die until late in the rotation. Retaining declining live trees, or recently-dead snags, ensures timely onset of decay.

- *Ensure that some large trees or snags are retained*—Although individual birds use a wide range of tree or snag sizes, they tend to select larger ones when available. Current data suggest that conifer cavity trees > 50 cm would accommodate most bird species, and most hardwood trees can be smaller (Bunnell and others 2002). Studies of vertebrate-forest relations have concentrated where trees are larger and more valuable, so existing data overestimate requirements where trees are smaller. A diameter > 30 centimeter will accommodate most bird species in less productive, inland forest types (Bunnell and others 2002). Some mammals select trees or snags > 50 centimeters in diameter (e.g., marten, black bear), and use down wood 50 to 150 centimeter in diameter (Davis 1996, Raphael and Jones 1997, USDA Forest Service 1996). Given how larger mammals use space, large pieces of down wood for such species can be well distributed across large areas. Large trees and snags provide nesting or denning sites longer than do small snags (Graham 1981, Morrison and Raphael 1993). However, smaller snags provide foraging sites, and many more foraging sites are needed than nesting sites.
- *Meet dead wood requirements for larger species in areas where the emphasis is not on intensive fiber production*—Binkley (1997) and Bunnell and others (1999a) reviewed economic and ecological advantages of zoning the intensity of fiber production. In some forest types, larger mammals prefer significant amounts (100 to 200 cubic meters/hectare or more) and sizes (> 50 centimeter diameter) of down wood (review in Lofroth 1993). Needs of those species are best provided in areas where late-successional attributes are being maintained. Provision of some large pieces of dead wood in forests where the dominant goal is fiber production may facilitate dispersal among areas of more favorable habitat.
- *Don't do the same thing everywhere*—Retention of trees in patches reduces safety risks of snag retention and windthrow (Coates 1997, Franklin and others 1997) and facilitates retention of a range of size and decay classes. It also concentrates recruitment of down wood. Debris piles are used by some vertebrates (Morris 1984, Raphael and Jones 1997), but scattered pieces of down wood favor other organisms. Dispersed retention of individual snags, or declining live trees intended to become snags, may be particularly advantageous for perching birds, and for territorial secondary users, such as, raptors and some small birds, but impact shrub nesters negatively by encouraging aerial predators (Vega 1993). Any single approach will disadvantage some group of species, so a range of practices is preferable if a range of species is to be sustained in an area.

- *Limit salvage logging after forest fires*—Fire suppression has reduced the area of recent burns favored by several vertebrates. If all vertebrates are to be sustained, salvage logging should not be performed over all burns, or the entire area of large burns.

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Appendix A—*Native cavity and downed wood using vertebrates breeding in forests in the Pacific Northwest and their state or provincial status.*

Common name	Scientific name	Cavity[2]	DW[3]	State or Province[1] BC	AB	WA	OR	CA
Amphibians								
Pacific giant salamander	*Dicamptodon tenebrosus*		X	R				
Arboreal salamander	*Aneides lugubris*		X					
Black salamander	*Aneides flavipunctatus*		X				S	
Clouded salamander	*Aneides ferreus*		X				S	
Coeur D'Alene salamander	*Plethodon idahoensis*		X	R				
Ensatina salamander	*Ensatina eschscholtzii*		X					
Western redback salamande	*Plethodon vehiculum*		X					
Reptiles								
Western skink	*Eumeces skiltonianus*		X					
Western fence lizard	*Sceloporus occidentalis*		X					
Ruber boa	*Charina bottae*		X	B			S	
CA mountain kingsnake	*Lampropeltis zonata*		X					
Racer	*Coluber mormon*		X					
Ringneck snake	*Diadophis punctatus*		X					
Sharptail snake	*Contia tenuis*		X	R	S			
Birds								
Order Anseriformes								
Barrow's goldeneye	*Bucephala islandica*	S					S	
Bufflehead	*Bucephala albeola*	S					S	
Common goldeneye	*Bucephala clangula*	S						
Common merganser	*Mergus merganser*	S						
Hooded merganser	*Lophodytes cucullatus*	S						
Red-breasted merganser	*Mergus serrator*	S						
Wood duck	*Aix sponsa*	S						

(*appendix A* continued)

				State or Province[1]				
Common name	**Scientific name**	**Cavity[2]**	**DW[3]**	**BC**	**AB**	**WA**	**OR**	**CA**
Order Falconiformes								
American kestrel	*Falco sparverius*	S						
Barred owl	*Strix varia*	S			S			
Boreal owl	*Aegolius funereus*	S			S	S		
Flammulated owl	*Otus flammeolus*	S		B		S		
Northern hawk owl	*Surnia ulula*	S						
Northern pygmy-owl	*Glaucidium gnoma*	S		B		S		
Northern saw-whet owl	*Aegolius acadicus*	S		B				
Spotted owl	*Strix occidentalis*	S		R	T	T	T	
Western screech-owl	*Otus kennicottii*	S		R/B				
Order Apodiformes								
Vaux's swift	*Chaetura vauxi*	S						
Order Piciformes								
Acorn woodpecker	*Melanerpes formicivorus*	P						
Black-backed woodpecker	*Picoides arcticus*	P			S	S		
Downy woodpecker	*Picoides pubescens*	wP						
Hairy woodpecker	*Picoides villosus*	P		B				
Lewis's woodpecker	*Melanerpes lewis*	wP		B		S		
Northern flicker	*Colaptes auratus*	wP						
Nuttall's woodpecker	*Picoides nuttallii*	wP						
Pileated woodpecker	*Dryocopus pileatus*	P			S	S		
Red-breasted sapsucker	*Sphyrapicus rubber*	P						
Red-naped sapsucker	*Sphyrapicus nuchalis*	P						
Three-toed woodpecker	*Picoides tridactylus*	P				S		
White-headed woodpecker	*Picoides albolarvatus*	wP		R		S		
Williamson's sapsucker	*Sphyrapicus thyroideu*	P		R\B				
Yellow-bellied sapsucker	*Sphyrapicus varius*	P						

(*appendix A* continued)

Common name	Scientific name	Cavity[2]	DW[3]	State or Province[1]				
				BC	AB	WA	OR	CA
Ash-throated flycatcher	*Myiarchus tyrannulus*	S						
Purple martin	*Progne subis*	S		R		S		
Tree swallow	*Tachycineta bicolor*	S						
Violet-green swallow	*Tachycineta thalassina*	S						
Boreal chickadee	*Poecile hudsonicus*	wP						
Chestnut-backed chickadee	*Poecile rufescens*	wP						
Mountain chickadee	*Poecile gambeli*	wP						
Plain titmouse	*Parus inornatus*	wP						
Siberian tit	*Parus cinctus*	wP						
Pygmy nuthatch	*Sitta pygmaea*	wP				S		
Red-breasted nuthatch	*Sitta canadensis*	wP						
White-breasted nuthatch	*Sitta carolinensis*	wP						
Brown creeper	*Certhia americana*	C		S				
Bewick's wren	*Thryomanes bewickii*	S						
House wren	*Troglodytes aedon*	S						
Winter wren	*Troglodytes troglodytes*	S	X					
Mountain bluebird	*Sialia currucoides*	S						
Western bluebird	*Sialia mexicana*	S				S		
Mammals Order Insectivora								
Common shrew	*Sorex cinereus*		X					
Dusky shrew	*Sorex monticolus*		X					
Pacific shrew	*Sorex pacificus*		X	R				
Pygmy shrew	*Sorex hoyi*		X					
Trowbridge's shrew	*Sorex trowbridgii*		X	B				
Order Chiroptera								
Big brown bat	*Eptesicus fuscus*	S						
California myotis	*Myotis californicus*	S						
Fringed myotis	*Myotis thysanodes*	S		B				
Hoary bat	*Lasiurus cinereus*	S						
Keen's long-eared myotis	*Myotis keenii*	S		R				
Little brown myotis	*Myotis lucifugus*	S						
Long-legged myotis	*Myotis volans*	S				S		

(*appendix A* continued)

Common name	Scientific name	Cavity[2]	DW[3]	State or Province[1]				
				BC	AB	WA	OR	CA
Northern long-eared myotis	*Myotis septentrionalis*	C		B	B	S		
Silver-haired bat	*Lasionycteris noctivagans*	S				S		
Southern red bat	*Lasiurus blossevilli*	S						
Yuma myotis	*Myotis yumanensis*	S						
Order Rodentia								
Creeping vole	*Microtus oregoni*		X					
Heather vole	*Phenacomys intermedius*		X					
Northern red-backed vole	*Clethrionomys rutilus*		X					
Southern red-backed vole	*Clethrionomys gapperi*		X	R/B				
Western red-backed vole	*Clethrionomys occidentalis*		X					
White-footed vole	*Phenacomys albipes*		X		S			
Columbian mouse	*Peromyscus oreas*		X					
Deer mouse	*Peromyscus maniculatus*		X					
Pinon mouse	*Peromyscus truei*		X					
Sitka mouse	*Peromyscus sitkensis*		X					
Douglas' squirrel	*Tamiasciurus douglasii*	S						
Least chipmunk	*Tamias minimus*		X	R				
Long-eared chipmunk	*Tamias quadrimaculatus*		X					
Northern flying squirrel	*Glaucomys sabrinus*	S						
Red squirrel	*Tamiasciurus hudsonicus*	S						
Sonoma chipmunk	*Tamias sonomae*		X					
Townsend's chipmunk	*Tamias townsendii*		X					
Western gray squirrel	*Sciurus griseus*	S				S		
Yellow-pine chipmunk	*Tamias amoenus*		X					
Order Carnivora								
Red fox	*Vulpes vulpes*		X					
Bobcat	*Lynx rufus*		X			S		
Lynx	*Lynx Canadensis*		X			S		
Ermine	*Mustela erminea*		X	R/B				
Fisher	*Martes pennanti*	S	X	B	S	S		
Least weasel	*Mustela nivalis*		X					

(*appendix A* continued)

Common name	Scientific name	Cavity[2]	DW[3]	State or Province[1]				
				BC	AB	WA	OR	CA
Long-tailed weasel	*Mustela frenata*			R	S			
American marten	*Martes Americana*	S	X			S		
Mink	*Mustela vison*		X					
Black bear	*Ursus americanus*	S	X	R				
Raccoon	*Procyon lotor*	S	X					

[1] R = red listed; B = blue listed; S = sensitive species; E = endangered species; T = threatened species; Sources include: Alaska Department of Fish and Game internet site as of July 1997 (www.state.ak.us/adfg/); British Columbia Ministry of Environment, Lands and Parks (1992, 1996); Alberta Environmental Protection Status of Wildlife internet site as of December 1996 (www.gov.ab.ca/env/fw/); Rodrick and Milner (1991) for Washington; Marshall and others (1996) for Oregon; and the U.S. Fish and Wildlife Service Division of Endangered Species internet site as of April 1999 for California. Other jurisdictions of the Pacific Northwest listed no species dependent upon cavity sites or downed wood.

[2] P = Primary Cavity Nester, wP = Weak Primary, S = Secondary Cavity Nester (obligate), C = Cave or Crevice; (may use cavities, especially during winter).

[3] Uses downed wood for breeding and/or feeding; X = Strongly Associated.

Summer and Fall Use of Logging Residue Piles by Female Short-tailed Weasels[1]

Kimberly A. Lisgo,[2] Fred L. Bunnell,[2] and Alton S. Harestad[3]

Abstract

Female short-tailed weasels *(Mustela erminea)* used piles of logging residue more than expected and used areas without logging residue less than expected when they were in 3-year-old regenerating aspen *(Populus tremuloides)* cutblocks during summer and fall ($P < 0.001$). Female weasels may prefer piles of logging residue because they offer greater amounts of food, larger numbers of rest sites, and greater availability of travel corridors. Our data indicate that food abundance, specifically the southern red-backed vole *(Clethrionomys gapperi),* best explains the preferential use of logging residue piles by female weasels. Recommendations for the management of logging residue piles are discussed.

Introduction

Downed wood provides structure in habitats of mustelids and small rodents, including secure travel corridors and, in winter, subnivian access and thermal cover. The importance of downed wood for mustelids, particularly marten *(Martes americana)* and fisher *(M. pennanti),* is well documented (Buskirk and Powell 1994, Buskirk and Ruggiero 1994, Corn and Raphael 1992) and is expressed in habitat quality as both amount of cover and available prey. For small rodents, downed wood can function as travel routes (Carter 1993, Maser and others 1979, Maser and Trappe 1984), provide fungal fruiting bodies for food (Maser and Trappe 1984, Rhoades 1986), and supply nest sites (Weaver 1996). Combined, these factors may encourage positive association of red-backed voles (*Clethrionomys* spp.) with downed wood (Nordyke and Buskirk 1991, Thompson 1996) through increased survivorship and reproduction. The relationship of weasels to downed wood is less clear. There are only a few anecdotal accounts that describe use of downed wood by short-tailed weasels *(Mustela erminea).* In areas that have been clearcut, logging provides substantial amounts of residual downed wood that can be dispersed or left in piles. Gyug (1994) reported that short-tailed weasels used cutblocks with logging residue piles more than those with none. Because of the shape and size of weasels, it is likely that the benefits of logging residue piles accrued to small rodents may apply to the

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short-tailed weasel (e.g., travel routes). As well, higher abundance of small rodents could attract weasels to downed wood as foraging sites.

Our objectives were to determine if female weasels, when they were in cutblocks, preferred logging residue piles to areas without logging residue piles; examine factors that could account for such behavior; and propose enhancement of short-tailed weasel habitat through management of logging residue piles.

Study Area

Our study area (54°58'N, 111°55'W), in the southern portion of the mixedwood boreal forest, is located at Owl River, approximately 300 kilometers northeast of Edmonton, Alberta. The mixedwood boreal forest is circumpolar. In Canada, it extends from northeastern British Columbia, through Alberta and Saskatchewan, to southeastern Manitoba. The province of Alberta contains approximately 40 percent or 290,000 square kilometers of Canada's mixedwood boreal forest (Rowe 1972).

The mixedwood boreal region is characterized by a complex mosaic of stands varying in age, species composition, and structure, interspersed with rivers, lakes, bogs, and fens. The dominant coniferous tree species are white spruce *(Picea glauca)* and black spruce *(P. mariana),* with balsam fir *(Abies balsamea),* jack pine *(Pinus banksiana)* and larch *(Larix laricina)* also present (Rowe 1972). Dominant deciduous species are trembling aspen *(Populus tremuloides)* and balsam poplar *(Populus balsamifera),* with lesser amounts of white birch *(Betula papyrifera)* (Rowe 1972). Although relatively pure stands of all these tree species exist, the most common later seral stages are a mix of species, most often trembling aspen, balsam poplar, and white spruce. The dominant natural disturbance regime in the mixedwood boreal forest is fire (Johnson 1992, Rowe 1961). Other disturbances include cutting of seismic lines for oil and gas exploration, white spruce saw-timber operations, harvesting of timber for pulp production, windstorms, and pathogens. These disturbances vary in size and contribute to the complex mosaic of stands that characterize the landscape.

Our study area is located within the Forest Management Area of Alberta Pacific Forest Industries Inc. (AlPac) and is located within two townships (Township 69 Range 13 W4M and Township 70 Range 13 W4M), each approximately 10 kilometers by 10 kilometers. The townships are dominated by jack pine stands (1930 origin), black spruce-larch mixed stands (1880 origin), and mature mixed and pure stands of trembling aspen and balsam poplar (1930-1950 origin). Large wet shrubby areas of dwarf birch (*Betula pumila* var. *glandulifera*), alder (*Alnus* spp.), and willow (*Salix* spp.) also are present. Pure stands of white spruce and mixed deciduous-coniferous stands are relatively uncommon. There are several small lakes in the area. Some agricultural land occurs adjacent to the southern edge of the study area. Portions of both townships were harvested by clearcutting and partial cutting for aspen and poplar in winter 1993/94. Based on Alberta Vegetation Inventory mapping (Alberta Forestry, Lands and Wildlife 1991), cutblocks range in size from 1 to 62 hectares and account for approximately 6.5 percent of the area. During our study, July to December 1996, cutblocks were densely vegetated with naturally regenerating aspen and poplar saplings, wild rose (*Rosa* spp.), herbs, and grasses.

The mean daily temperature for this region is 3.9 to 10.9 degrees Celsius in summer (May-September) and -1.1 to -22.4 degrees Celsius in winter (October-

April). The annual mean precipitation is 432.3 millimeters including 131.5 centimeters of snow. Major snowfall months are November to April with a mean monthly snowfall of 11.9 to 25.0 centimeters during this period (Environment Canada 1998).

Methods

Radio-tagging and Telemetry

During February-December 1996, we live-trapped weasels in wooden box traps modified from King (1973) and insulated with cotton. The traps were baited with bacon or carcasses of white laboratory mice and placed systematically in cutblocks, but near downed wood or other cover. We used data from four female weasels in this analysis (females 1 to 4). All four females were adults (> 1 year of age) and were known to inhabit cutblocks prior to collaring. Each female was fitted with a Holohil® MD2C[4] transmitter weighing 2-3 grams, < 4 percent of an adult female's body weight. As recommended by King (1989), we held weasels in-hand when attaching collars rather than anaesthetizing them. We monitored the four females between July and December 1996 and located them by radio-triangulation (White and Garrott 1990) from fixed telemetry stations. We recorded at least three bearings from separate stations for each location. After we determined a general location, we approached the site to confirm activity (i.e., resting versus foraging), specific location, and habitat type. We flagged the site and returned later to locate it using a hand-held global positioning system (GPS). The GPS data were corrected to ± 1 meter. Because of equipment problems, telemetry sampling was sometimes erratic. In general, females were located every 1 to 2 days. Female weasels often damaged their transmitters, and 1-week periods without locations were not uncommon. We attempted to obtain the locations over the 24-hour day, but despite our efforts and because of safety issues working at night, daytime locations dominate our data.

We used variations in signal strength to deduce activity of radio-collared weasels. Hunting or traveling activity was indicated by changes in the volume of the radio signal. When inactive, the signal volume remained constant. We identified an inactive location using zone of receiver (i.e., when the signal could be heard on the receiver without an external antenna). We moved to the edge of the signal range where reception was most sensitive to changes in the weasel's location. We listened to the signal for 15 minutes. If a change in signal strength was not observed, we deemed the weasel inactive.

Logging Residue Piles

We defined logging residue piles (LRPs) as the tops and branches of felled trees, dispersed along the main road, and spurs passing through cutblocks. We determined the areas of LRPs in four cutblocks used by females 1 to 4. The cutblocks were all harvested for trembling aspen *(Populus tremuloides)* during winter, 1993-94, using dispersed retention with 1-2 percent of the trees left uncut and the logging residue distributed along access roads in the cutblocks. Approximately 35-68 meters of main road and spurs occurred per hectare of cutblock.

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

In May 1997, we walked the perimeter of each LRP taking Universal Transverse Mercator (UTM) coordinates via hand-held GPS every 5 seconds or approximately every 2-5 meters. The GPS point data were corrected to ± 1 meter. We converted the point data into vector polygons using Arc/Info Version 7.1 (ESRI 1997) and imported the vector polygons into ArcView version 3.1 (ESRI 1996). We calculated the area of LRPs and cutblock habitat available for use within each female's home range using a raster overlay of home range, LRP polygons, and digitized Alberta Vegetation Inventory maps with a 0.1- x 0.1-meter raster resolution. We defined home range as "the area traversed by an individual during its normal activities of food gathering and resting within the period when sampling occurred" (Lisgo 1999). We calculated home ranges using a fixed kernel estimator based on a 95 percent utilization distribution (Lisgo 1999).

Use of Logging Residue Piles by Weasels

We tested selective use of LRPs in cutblocks using the log-likelihood ratio (Zar 1984). Availability of cutblocks and LRPs for each weasel was based on their respective area within a female's home range. We used both active (i.e., hunting or traveling) and inactive (i.e., resting or consuming prey) observations in the analyses.

Small Rodent Abundance Estimates

We live-trapped small rodents in two cutblocks, Sites 1 and 2, that 3 female weasels (females 2 to 4) were known to use. We placed four Multi-capture Tin Cat® live traps 25 meters apart in a diamond configuration with an additional trap placed in the centre (five traps in total). We placed six trap arrays in each cutblock: three trap arrays in areas of LRPs and three trap arrays in areas of no-LRPs. We trapped each cutblock for three nights from October 4 to 6, 1996. We identified each small rodent to species and then sexed, weighed, marked it with picric acid, and released it. Although the rodents were not uniquely marked, we later recorded the number of marked (previously captured) and unmarked animals during trapping sessions. We estimated abundance for four areas: 1) Site 1 areas of LRPs; 2) Site 1 areas of no-LRPs; 3) Site 2 areas of LRPs; and 4) Site 2 areas of no-LRPs. In each case, data from the three tray arrays were pooled.

We used the Schumacher and Eschmeyer method, a version of the Schnabel method, to estimate the abundance of small rodents with 95 percent confidence limits (Krebs 1989). This method estimates the abundance for a closed population (i.e., population size is constant without recruitment or loss). It is appropriate for this study because the trapping occurred over a short period. The Schumacher and Eschmeyer method distinguished two types of individuals: 1) marked individuals caught previously at least once; and 2) unmarked individuals not caught previously. We calculated 95 percent confidence limits for each population estimate using a Poisson distribution as recommended for cases in which total number of recaptures is less than 50 (Krebs 1989).

Results

Area of Logging Residue Piles and Their Use by Weasels

On average, 57 percent (112/198) of the females' locations were in cutblocks and 43 percent (86/198) in uncut forest and shrubby habitats. Within cutblocks, the area of LRPs in female home ranges varied from 2.03 to 3.93 hectares *(table 1).* When in cutblocks, all four females preferred areas of LRPs to areas without LRPs (P < 0.001, *table 2).* Collectively, observations of inactive females in areas with LRPs and without LRPs account for only a small proportion of the data, 11 percent and 18 percent, respectively *(table 2).*

Table 1—*Cutblock area found within the home range of each female weasel and area within the cutblock designated as areas with logging residue piles (LRPs) or without logging residue piles (no-LRPs) based on GIS analyses.*

Weasel	Home range size (hectare)	Cutblock area (hectare)	Area of no-LRPs (hectare)	Area of LRPs (hectare)	Percentage LRPs in cutblock area
Female 1	82.6	24.43	22.40	2.03	8.3
Female 2	94.8	34.70	32.59	2.11	6.1
Female 3	65.5	32.09	28.16	3.93	12.2
Female 4	76.8	23.53	21.21	2.41	10.2

Table 2—*Selective use of logging residue piles within cutblocks by female short-tailed weasels in the mixedwood boreal forest of central Alberta, based on the log-likelihood ratio. Values in parentheses are the number of inactive observations in areas with logging residual piles (LRPs) and without logging residue piles (no-LRPs).*

Weasel	Observed locations in LRPs	Observed locations in no-LRPs	Expected locations in LRPs	Expected locations in no-LRPs	Log-likelihood ratio	P
Female 1	11 (4)	7 (0)	1.5	16.5	31.82	< 0.001
Female 2	14 (0)	18 (5)	2.0	30.0	36.09	< 0.001
Female 3	21 (2)	34 (7)	6.7	48.3	24.10	< 0.001
Female 4	7 (0)	6 (0)	1.3	11.7	15.55	< 0.001

Abundance of Small Rodents

We caught three species of small rodents: southern red-backed voles *(C. gapperi),* meadow voles *(Microtus pennsylvanicus),* and deer mice *(Peromyscus maniculatus) (table 3).* We captured relatively few meadow voles with most individuals appearing in traps on the last trap night. Estimates of abundance for red-backed voles showed a trend for greater numbers in areas of LRPs, while estimates of abundance for deer mice did not differ between areas of LRPs and no-LRPs *(fig. 1).*

Table 3—*Species and the number of captured and recaptured small rodents in areas with logging residue piles (LRPs) and without logging residue piles (no-LRPs) for Sites 1 and 2 from October 4-6, 1996 in the mixedwood boreal forest of central Alberta.*

		Site 1		Site 2	
Treatment	**Species**	**No. captured**	**No. recaptured**	**No. captured**	**No. recaptured**
no-LRPs	red-backed vole	33	11	13	3
	deer mouse	33	16	38	14
	meadow vole	2	0	0	0
LRPs	red-backed vole	42	7	29	8
	deer mouse	35	14	31	11
	meadow vole	5	0	2	0

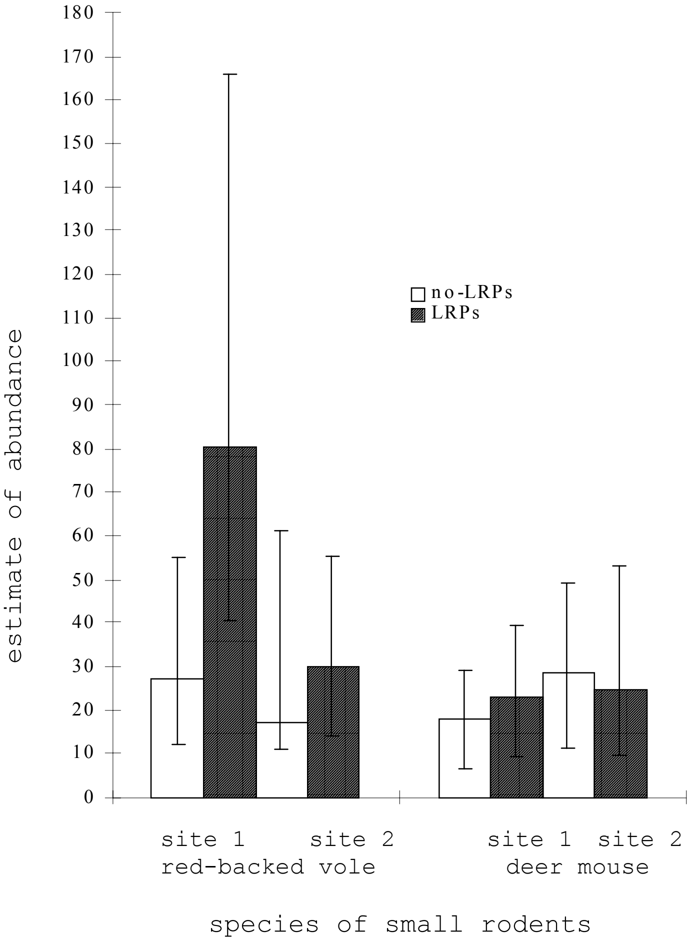

Figure 1—Abundance estimates of southern red-backed voles and deer mice with 95 percent confidence limits based on the Schumacher and Eschmeyer method (Krebs 1989), October 4-6 1996, in areas of no logging residue piles (no-LRP) and logging residue piles (LRP), in regenerating aspen cutblocks (harvested winter 1993/94), in the mixedwood boreal forest of central Alberta.

Discussion

There are two features to our study that could potentially bias our results. First, the high proportion of daylight locations in our data set may bias our estimates of habitat use. However, in summer, North American and European weasels are predominantly diurnal in activity (Debrot and others 1985, Erlinge 1979, Samson and Raymond 1995). Second, it is also possible that radio-tagging compromised the behavior of collared weasels and that these weasels do not accurately represent the population. White and Garrott (1990) stress the importance of testing the effect of radio-tagging on study animals. Lisgo (1999) found that collared weasels did not suffer nutritionally; however, we do not know if the normal hunting behavior of weasels was affected by the presence of a radio-collar. For example, the increased diameter of a weasel's neck caused by a radio-collar may have limited the size of mouse and vole tunnels that could be explored.

In the mixedwood boreal forest of Alberta, four female weasels preferentially used areas with LRPs in cutblocks during summer and fall. They spent three to seven times more time in LRPs than expected. Although our sample size was small, all females showed similar behavior. Also, our results are consistent with the behavior of weasels in southern British Columbia during winter (Gyug 1994). We think that female weasels may selectively use areas with LRPs for three reasons: the amount of food; availability of rest sites; and availability of travel corridors with security cover. Our findings suggest that abundance of food, specifically red-backed voles, best explains the preferential use of LRPs by female weasels.

We think that food resources promoted use of LRPs because LRPs had a higher abundance of prey. Abundance of prey, at least for Site 1 and particularly red-backed voles, tended to be higher in LRPs than in areas without LRPs. Deer mice were distributed evenly throughout both cutblocks. Lisgo (1999) found red-backed voles were an important component of the weasel's diet, significantly preferred over deer mice ($P < 0.05$). Higher abundance of prey, especially red-backed voles, in LRPs would reduce hunting effort for weasels and make these areas attractive as foraging sites.

Other studies also have found positive associations between red-backed voles and downed wood (Nordyke and Buskirk 1991, Thompson 1996). In the mixedwood boreal forest, Roy and others (1995) found both red-backed voles and deer mice positively associated with downed woody material. Roy and others (1995) also concluded that deer mouse populations are flexible in their habitat requirements while red-backed vole populations are less so and "select areas of dense shrubs with abundant downed woody material." The flexible habitat requirements of deer mice explain their even distribution throughout the cutblocks. The red-backed voles positive association with downed wood explains their trend for greater abundance in LRPs.

In our study area, Weaver (1996) found that red-backed voles and deer mice nested beneath LRPs, rotting downed wood, and the base of stumps and snags in cutblocks. Female weasels also rested in LRPs; thus, rest site availability may also encourage the use of LRPs by female weasels. Weasels rely on natural cavities or the nests of other species for rest sites (King 1989). Hence, we expect more resting activity by female weasels in LRPs due to a greater availability of nests, which may be associated with the higher abundance of small rodents. It does not appear, however, that LRPs are necessary for female weasels to find suitable rest sites in cutblocks because female weasels also rested at the bases of stumps and snags in portions of cutblocks without LRPs (Lisgo 1999).

The response of weasels to LRPs may be an anti-predator behavior by which they choose travel routes with the least risk of predation (Harestad 1991). Although LRPs may function as secure travel corridors for female weasels, we think it unlikely that this would be the sole attractant for females because dense vegetation throughout the cutblocks provided alternative sources of security and thermal cover. However, LRPs may facilitate movements of weasels by providing travel routes less hindered by dense vegetation while providing security cover.

Despite our small sample size, this information on habitat use is valuable to forest managers. There are few data on the ecology of the short-tailed weasel in North America or the effects of silvicultural practices on the behavior of weasels. However, caution must be used when applying our findings to weasels outside our study area, and in particular, to male weasels. The behavioral response of male weasels to the presence of logging residue piles is not known and, based on work in our study area, males use the landscape differently than females (Lisgo 1999).

Caution is also necessary when interpreting the responses of small rodents to LRPs. First, the level of replication was small and our findings for small rodents may be restricted to the cutblocks that we sampled. Second, the sampling period was short and may not be representative of the full 6 months during which female weasels were observed.

Management Recommendations

Female weasels preferred areas with LRPs that were used for resting, hunting, and possibly travel routes. Small rodent abundance, in particular red-backed voles, suggests that prey abundance may be a factor promoting the use of LRPs by females. At the time of our study (3 years post-harvest), LRPs were not essential for providing suitable rest sites because female weasels also rested in portions of cutblocks without LRPs. Based on our findings, LRPs tend to support a higher abundance of red-backed voles and appear to be a beneficial attribute of 3-year-old regenerating aspen cutblocks in our study area.

Because female short-tailed weasels prefer logging residue piles, timber-harvesting practices could be altered to provide residual downed wood. Besides amount, distribution of logging residue piles may be important to supplying suitable habitat for both small rodents and weasels. Logging residue can be dispersed, piled, or removed from a site depending on silvicultural prescriptions and harvesting methods. We recommend that LRPs be retained and distributed linearly along main roads and spurs to ensure they occur in home ranges of several female weasels. Many other wildlife species inhabit cutblocks and the habitat quality for some likely would be diminished if this recommendation was applied throughout the landscape. To sustain all wildlife species, the same practices should not be used everywhere (Bunnell and others 2002). A diverse approach, managing for multiple species, is more appropriate for sustaining wildlife in the mixedwood boreal forest. Moreover, the data provided are based on a 6-month study, and weasel home ranges fluctuate with prey abundance (Erlinge 1977). Declines or increases in abundance of prey may result in expansion or contraction of home range size and could change use of habitats by weasels. Also, over time, the reduction of LRPs through decay may lower the suitability of cutblocks as habitat for weasels. Lastly, because of the mixedwood boreal forest's diverse landscape, the habitats studied are not representative of the entire mixedwood boreal forest. Recommendations suitable for the forest types in our study area may be inappropriate for other locations, such as those dominated by older mixedwood stands.

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Dead Wood and the Richness of Small Terrestrial Vertebrates in Southwestern Oregon[1]

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Abstract

In southwestern Oregon, 24 mature forest stands were used to test the hypothesis that species richness of small terrestrial vertebrates is positively correlated with dead wood volume, and to compare dead wood loads between capture and non-capture sites for species encountered. Dead wood was separated into two components: coarse woody debris (CWD)—defined as down wood of any length ∃ 10 cm in diameter—and snags, defined as standing dead wood ∃ 0.5 m in height and ∃ 25 cm in diameter. The volume of CWD in stands ranged from 50 to 860 m^3/ha and snag volumes ranged from 10 to 240 m^3/ha. Small terrestrial vertebrates numbered between 8 and 20 species per stand based on a pitfall sampling effort of approximately 3,600 trap nights per stand over 2 years. Regression analysis revealed that the species richness of all terrestrial vertebrates taken as a single group increased with increasing volumes of CWD. Viewed as separate taxonomic groups, species richness of small mammals, insectivores, and amphibians all correlated positively with CWD volume; rodent richness showed no significant relationship with CWD. None of the vertebrate groups disclosed significant correlations between species richness and snag volume. Although some individual species at the stand scale did not appear to associate with dead wood, the study results do not preclude the importance of dead wood as a microhabitat feature. The results of this study predict that if all stands are managed to Federal CWD targets in southwestern Oregon, the full component of small terrestrial vertebrates typical of Pacific Northwest forests will not be realized.

Introduction

Many species of wildlife use dead wood as breeding habitat, for cover, or as a source of prey (Bartels and others 1985). In the Pacific Northwest, regulations exist for the management of dead wood on forestlands for the purpose of accommodating wildlife (Oregon Department of Forestry 1991, USDA and USDI 1994). Despite specific number, dimensions, and decay class requirements, dead wood targets frequently vary little for vastly different forest community types partly because of limited available data on natural dead wood conditions and threshold levels of snags and down wood needed to maintain species diversity.

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Appropriate amounts of dead wood for managed forests continue to be debated. Safety and economic concerns often are at odds with wildlife needs particularly when snags and down wood are created from green trees to meet management objectives, thereby compromising potential revenue (Hope and McComb 1994, Wick and others 1985). Compounding the issue is a poor database correlating wildlife diversity and abundance with varying levels of dead wood, and hence, a lack of basic information on which to base reliable dead wood goals (McComb and Lindenmayer 1999). Therefore, research is necessary to identify critical levels of dead wood needed to support diverse forest wildlife communities, ascertain the level of dead wood above which diversity is no longer served, and evaluate whether current dead wood guidelines are adequately meeting the needs of the wildlife for which they were created. In short, quantification of the relationship between amount of dead wood and small terrestrial vertebrates will allow explicit recognition of the biological costs and benefits of establishing a given dead wood target.

The objectives of this study were to test the hypothesis that species richness of small terrestrial vertebrates is positively correlated with dead wood volume, and to shed light on richness trends by comparing dead wood loads between capture and non-capture sites for species encountered. These relationships were tested with data from upland forest stands in southwestern Oregon.

Methods

Study Area

Twenty-four 13-ha Douglas-fir *(Pseudotsuga menziesii)* dominated mature upland stands from the Umpqua National Forest in southwestern Oregon were selected for study *(table 1)* (see Aubry and others [1999], and Abbott and others [1999] for site selection criteria). Six stands are located in each of four separate areas with stands within areas frequently adjacent. The stands generally have southeast to southwest aspects and slopes ranging from flat to approximately 60 percent. Most stands have a history of thinning or salvage logging. The stands make up the Oregon component of DEMO (Demonstration of Ecosystem Management Options), a USDA Forest Service funded study initiated in the 1990s to examine the responses of diverse groups of forest organisms and processes to variation in the amount and/or pattern of residual live trees after harvest (Halpern and Raphael 1999). Information presented represents pre-harvest conditions in the overall DEMO study plan.

Vertebrate Sampling

An 8 x 8 or 7 x 9 grid with 40-m spacing between grid points was established as the template for animal trapping and dead wood sampling (see Aubry and others [1999)] for grid spacing justification). Pitfall traps constructed of 2 number 10 cans (final dimensions: 15-cm diameter x 72-cm length) were sunk into the ground at each grid point and operated as removal traps for 28 consecutive days in October and November 1995 and 1996 (approximately 1,800 trap nights per stand per year) to assess small terrestrial mammal and amphibian abundance. Although time constrained searches (TCS) often are recommended for sampling amphibians directly utilizing down wood, pitfall traps have the benefit of more successfully sampling the array of species present (Bury and Corn 1988). In addition, TCS are not always more effective than pitfall traps (Maguire, pers. observ.). Captured animals were transported to the laboratory and identified.

Voucher specimens from this study are housed in museums at Harvard in Cambridge, Massachusetts; Shippensburg University in Pennsylvania; Texas A & M in College Station; and the University of Alaska in Fairbanks. Museum staff verified species.

Table 1—*Pre-harvest characteristics of the 24 DEMO stands in the Umpqua National Forest in southwestern Oregon.*

Block/stand no.	Stand age (yr)	Elevation (m)	BA[1] (m^2/ha)	Mean DBH[2](cm)	Snags (m^3/ha)	CWD[3] (m^3/ha)
Watson Falls						
1	110	1,312	46.90	61	120.9	188.7
2	110	946	42.99	51	83.1	67.4
3	110	1,159	42.99	51	25.0	190.9
4	130	1,312	58.62	61	109.4	185.8
5	130	946	42.99	51	41.5	142.6
6	130	946	58.62	51	48.2	96.6
Little River						
1	400-520	1,281	128.74	122	193.2	547.9
2	250-300	1,373	91.95	91	175.3	205.4
3	300	1,281	103.45	97	70.9	219.0
4	200-250	1,312	80.46	114	240.1	183.2
5	300	1,251	103.45	97	100.0	261.7
6	225-325	1,312	74.71	86	25.7	94.1
Layng Creek[4]						
1	80	763	35.86	46	34.1	425.8
2	60	671	27.82	41	100.4	383.9
3	80	763	35.86	46	38.3	565.2
4	60	671	30.34	43	54.0	862.1
5	65	488	27.82	41	11.0	262.6
6	80	671	28.05	48	38.6	374.5
Dog Prairie						
1	165	1,647	68.97	61	78.7	58.4
2	165	1,647	68.97	61	54.8	91.1
3	165	1,525	68.97	61	125.5	180.0
4	165	1,647	68.97	61	57.1	62.4
5	165	1,647	68.97	61	28.4	50.5
6	165	1,525	68.97	61	142.5	232.9

[1] BA = basal area
[2] DBH = diameter at breast height
[3] CWD = coarse woody debris
[4] All six stands are second growth.

Dead Wood Sampling

Dead wood was sampled on an average of 42 (range: 32 to 64) grid points per stand during snow-free months in 1994 through 1996. Selection of points was based on planned harvest treatments (Halpern and others 1999). Snags were counted on a circular 0.08-ha (15.96-m radius) plot centered on each of 1,037 sampling points, and diameters, height classes, and decay classes (Cline and others 1980) were recorded. Snags were defined as standing dead wood ∃ 25 cm in diameter and ∃ 0.5 m in height. Coarse woody debris (CWD) was measured (Brown 1974) at 851 sampling stations across the 24 stands using four 6-m transects radiating out at 90^o angles 4 meters from each sample point. Diameter of CWD at the point of intersection with the line transects, length, and decay class were recorded. CWD was defined as down wood of any length ∃ 10 cm in diameter. Snag and CWD volume estimates were calculated for each stand.

Analytical Methods

The number of species found in a location is tied to the number of captures (Rosenzweig 1995), i.e., the likelihood of encountering rare species increases with increasing sample size. When comparing species richness across sites where captures are unequal, the sample issue can be overcome by standardizing counts as in the rarefaction method outlined in Krebs (1989). In this richness estimation method, the number of species within each stand is predicted from a set number of randomly sampled individuals taken from the population. In this study, the mid-value from the range of stand captures for each vertebrate group was used to compute expected richness estimates by the rarefaction method.

Relationships between dead wood volume across the 24 stands and species richness estimates for standardized captures were examined by regression analysis. Both linear and log model forms were explored. To examine individual species associations with CWD volume that contributed to the richness trends observed at the stand level, Welch's approximate-t for unequal variance (Zar 1984) was used to test for differences in CWD volumes between capture and non-capture sites of each species. Siskiyou and Townsend's chipmunks (*Tamias siskiyou* and *T. townsendii*, respectively), northern flying squirrels *(Glaucomys sabrinus),* and ermines *(Mustela erminea)* were excluded from t-test analysis because pitfall traps are not the best method for capturing these species; and other methods employed in the DEMO study showed that these species occurred on some sites additional to those on which they were captured in pitfalls (Lehmkuhl and others 1999). Significance was tested at ∀ # 0.05.

Results and Discussion

Dead Wood

The volume of CWD in stands ranged from approximately 50 to 860 m^3/ha *(table 1).* These amounts represent volumes approximately 5 to 80 times the amount mandated by the Northwest Forest Plan (USDA and USDI 1994) for the Umpqua National Forest, but they are within the previously recognized range for terrestrial forest ecosystems (Harmon and others 1986).

Despite past salvage and selective harvest in the stands, CWD volumes still tracked the chronosequence "U"-shaped trajectory predicted by Spies and Franklin (1988) and observed in a variety of vegetation types for naturally regenerated forests (e.g., Agee and Huff 1987, McCarthy and Bailey 1994, Spies and others 1988, Sturtevant and others 1997, Wells and Trofymow 1997); that is, the largest CWD volumes are associated with both the youngest and the oldest stands *(fig. 1).* High numbers and volumes of down wood occur early in stand development after a catastrophic disturbance and in old-growth forests as dead wood accumulates (Spies and others 1988). Human disturbance in these forests did not significantly alter this pattern.

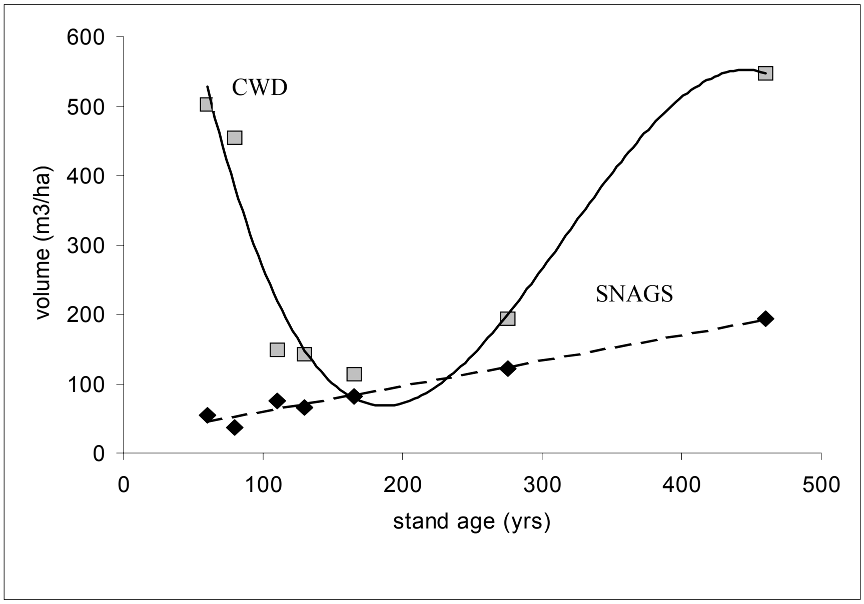

Figure 1—Mean stand volumes of coarse woody debris (CWD) and snags across stand ages for the 24 stands presented in *table 1.* Age groupings are 60/65, 80, 110, 130, 165, 275 (200-325), and 460 (400-520) years.

Snag volumes ranged from 10 to 240 m^3/ha across stands. Spies and Franklin (1988) also predicted a "U"-shaped developmental trajectory for snags in addition to CWD, but this pattern was not observed in these stands *(fig. 1),* possibly due to significant sacrifice or salvage of snags during past harvesting or the lack of snags during stand establishment. Nonetheless, similar non-"U" trends for snag volume have been found in other forest types (Sturtevant and others 1997, Tyrrell and Crow 1994). Snags and CWD volumes were poorly correlated ($r^2 = 0.001$, $p = 0.87$).

Species Richness

Regression analysis revealed that the species richness of all terrestrial vertebrates taken as a single group increased with increasing volumes of CWD and all dead wood (snags and CWD), but had no significant relationship with snag volume *(table 2).* Small mammals taken as a group, insectivores, and amphibians all reflected the same trends. The significance and linear relationship between richness and total dead wood volume was impacted by the substantial CWD component of total dead wood. Rodent richness was not correlated with any measure of dead wood volume.

Table 2—*Best fit regression models for the relationship between a variety of dead wood volumes and species richness of small terrestrial vertebrates estimated from the rarefaction technique (Krebs 1989). Species richness was estimated for the sample sizes in parentheses; sample sizes represent the mid-value of captures across 24 stands in the Umpqua National Forest, Oregon.*

Coarse woody debris volume (m^3/ha)

Species group	Model form[1]	r^2	p
All vertebrates (n = 326)	log (SR) = 0.785 + 0.160 log (CWD)	0.42	0.0007
All mammals (n = 301)	log (SR) = 0.797 + 0.101 log (CWD)	0.32	0.004
Rodents (n = 117)	log (SR) = 0.451 + 0.105 log (CWD)	0.14	0.07
Insectivores (n = 212)	log (SR) = 0.507 + 0.109 log (CWD)	0.28	0.009
Amphibians (n = 20)	log (SR) = -0.152 + 0.289 log (CWD)	0.33	0.003

Snag volume (m^3/ha)

Species group	Model form	r^2	p
All vertebrates (n = 326)	SR = 14.890 - 0.007 SNAG	0.02	0.48
All mammals (n = 301)	SR = 11.203 - 0.006 SNAG	0.05	0.30
Rodents (n = 117)	SR = 5.559 - 0.007 SNAG	0.12	0.09
Insectivores (n = 212)	SR = 5.905 - 0.002 SNAG	0.01	0.59
Amphibians (n = 20)	log (SR) = 0.311 + 0.103 log (SNAG)	0.04	0.33

Total dead wood volume (m^3/ha)

Species group	Model form	r^2	p
All vertebrates (n = 326)	log (SR) = 0.744 + 0.166 log (DW)	0.30	0.005
All mammals (n = 301)	log (SR) = 0.786 + 0.099 log (DW)	0.20	0.03
Rodents (n = 117)	log (SR) = 0.481 + 0.086 log (DW)	0.06	0.24
Insectivores (n = 212)	log (SR) = 0.480 + 0.113 log (DW)	0.20	0.03
Amphibians (n = 20)	log (SR) = -0.296 + 0.329 log (DW)	0.29	0.007

[1] SR = species richness = number of species estimated for a sample of n individuals; CWD = coarse woody debris volume; SNAG = snag volume; DW = total dead wood volume = CWD + SNAG volumes.

The results indicate that CWD volume is a better predictor of species richness at the stand level for small terrestrial vertebrates than either snag or total dead wood volumes in southwestern Oregon, even though snags provide a future source of down wood (Spies and others 1988). Many amphibians and mammals exploit snag cavities, flaking bark on snags, or insect and fungal food resources inhabiting snags (Dupuis and others 1995); but for many small terrestrial vertebrates, the absence of snags does not appear to be a limiting factor (Bunnell and others 1997).

Mammals represent the largest number of terrestrial vertebrate species associated with down wood (Brown 1985). Although species abundance may increase as dead wood abundance increases, many mammalian species that use down wood are not believed to require it (Bunnell and others 1997). The exception may be the insectivores. Down wood and insect levels often are tightly linked (e.g., Torgersen and Bull 1995), and insect outbreaks frequently are associated with unnaturally high levels of dead wood resulting from active fire suppression (Campbell and Liegel 1996). Because of the insect/dead wood linkage, animals that primarily consume insects, such as the insectivores, often have close ties to CWD, as is evident in this study. Conversely, insects represent only a portion of most rodent diets, and rodent richness was not strongly tied to down wood.

Amphibians also feed on insects, and they too had richness levels significantly correlated with CWD volume. In addition, amphibians, particularly salamanders, require moist habitat conditions, and the stable, moist micro-environment provided by the space beneath logs or the decomposing interior of logs is well suited to their life requisites (Bury and Corn 1988, Corn and Bury 1991a, DeMaynedier and Hunter 1995).

Individual Species

The number and type of animal species encountered varied widely across the 24 stands *(table 3).* Twenty-nine species were captured, including 7 salamanders, 2 frogs, 6 insectivores, 13 rodents, and 1 carnivore. The number of species in any stand ranged from 8 to 20, a richness range consistent with other studies (Bury and Corn 1988, Gomez and Anthony 1998).

With the exception of the rough-skinned newt *(Taricha granulosa)* and the spotted frog *(Rana pretiosa)*—species that both spend a major portion of their lives in or near water—previous studies suggest that the remaining seven species of amphibians associate with down wood when on land (Brown 1985, Bury and Corn 1988, Bury and others 1991, Corn and Bury 1991a, Stelmock and Harestad 1979). To evaluate the consistency of these relationships, CWD volumes between capture and non-capture stands for each species were tested for differences. Results did not always reflect the trends noted above. Dunn's salamander *(Plethodon dunni)* and western red-backed salamander *(P. vehiculum)* were captured on stands with greater volumes of CWD than non-capture stands. This positive association with down wood also extended to the rough-skinned newt. Conversely, Pacific treefrog *(Pseudacris regilla)* was located on stands with less CWD. Species that did not express significant relationships with down wood include clouded salamander *(Aneides ferreus),* northwestern salamander *(Ambystoma gracile),* and Pacific giant salamander *(Dicamptodon tenebrosus).* The spotted frog and ensatina *(Ensatina eschscholtzii)* were not analyzed because spotted frog was captured on only one stand while ensatina was captured on all stands but one *(table 3).*

Insectivores as a group were encountered more frequently than amphibians *(table 3).* Both the Trowbridge's and Pacific shrews *(Sorex trowbridgii* and *S. pacificus*, respectively) were present in all stands, and the vagrant shrew *(S. vagrans)* was located in all but one stand. Trowbridge's shrew is the most common shrew in Pacific Northwest forests west of the Cascade crest (Carey and Johnson 1995, Gomez and Anthony 1998); however, Dalquest (1941) stated that it is rarely found when the vagrant shrew is present. The results of the current study document the consistent overlap of Trowbridge's and vagrant shrews. Some research suggests that the vagrant shrew prefers moist open areas (Gomez and Anthony 1998, Hawes 1977) and is uncommon or absent in Douglas-fir forests (Terry 1981). These findings are inconsistent with the results of this study as all 23 sites where the vagrant shrew was found were upland Douglas-fir stands *(table 1).* Although some past research indicates that the vagrant shrew does indeed inhabit forested areas (e.g., Corn and Bury 1991b, Hooven and Black 1976), this earlier work has been met with skepticism because of the lack of voucher specimens (Verts and Carraway 1998) and earlier confusion concerning the taxonomic status of the species (Carraway 1990).

Table 3—*Species of terrestrial vertebrates captured in pitfall traps in 24 stands located in 4 blocks across the Umpqua National Forest in southwestern Oregon. Number 1 indicates that the species was captured; 0 represents no capture.*

	Research blocks Stand No.			
	Watson Falls	**Little River**	**Layng Creek**	**Dog Prairie**
	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6	1 2 3 4 5 6
Amphibians				
Salamanders				
Ambystoma gracile	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 0 1 1	1 1 1 0 0 1
Aneides ferreus	0 0 0 0 0 0	1 0 0 1 1 1	1 1 0 0 1 1	0 0 0 0 0 1
Dicamptodon tenebrosus	0 0 0 0 0 0	1 0 1 0 1 1	1 1 0 1 0 0	0 0 0 0 0 0
Ensatina eschscholtzii	1 1 1 1 1 1	1 1 1 1 1 0	1 1 1 1 1 1	1 1 1 1 1 1
Plethodon dunni	0 0 0 0 0 0	0 0 0 0 0 0	0 1 1 0 0 1	0 0 0 0 0 0
Plethodon vehiculum	0 0 0 0 0 0	0 0 0 0 0 0	1 1 1 1 1 1	1 0 0 0 0 0
Taricha granulosa	0 1 1 1 1 1	1 0 1 1 1 1	1 1 1 1 1 1	0 0 0 0 0 0
Frogs				
Pseudacris regilla	0 1 0 0 1 0	0 0 0 0 0 0	0 0 0 0 0 0	0 1 0 0 0 0
Rana pretiosa	0 0 0 0 0 0	0 1 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0
Mammals				
Insectivores				
Neurotrichus gibbsii	1 1 1 1 1 1	1 1 1 0 1 1	1 1 1 1 1 1	0 1 1 0 1 1
Scapanus orarius	1 0 1 0 0 0	0 0 1 1 0 0	1 1 1 1 1 1	0 1 0 1 0 1
Sorex bendirii	0 0 0 0 0 0	0 1 0 1 1 0	1 1 1 1 1 1	0 1 0 0 0 0
Sorex pacificus	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Sorex trowbridgii	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Sorex vagrans	1 1 1 1 1 1	1 1 0 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Rodents				
Arborimus albipes	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 1 1 1	0 0 0 0 0 0
Arborimus longicaudus	0 0 0 0 0 0	1 0 1 0 1 1	1 1 1 0 0 0	0 1 0 0 0 0
Clethrionomys californicus	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Glaucomys sabrinus	0 0 0 0 0 0	1 0 1 1 0 0	0 0 1 0 1 1	0 0 1 0 0 0
Microtus oregoni	1 1 1 1 1 1	1 1 0 1 1 1	1 1 0 1 1 1	1 1 1 1 1 1
Microtus richardsoni	0 0 0 0 0 0	1 0 0 0 0 0	0 0 1 0 1 1	1 0 0 0 0 0
Microtus townsendii	0 0 0 0 0 0	0 1 0 1 1 1	0 0 0 0 1 1	0 0 0 1 0 0

(*table 3* continued)

	Research blocks Stand No.			
	Watson Falls 1 2 3 4 5 6	**Little River** 1 2 3 4 5 6	**Layng Creek** 1 2 3 4 5 6	**Dog Prairie** 1 2 3 4 5 6
Peromyscus maniculatus	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1	1 1 1 1 1 1
Phenacomys intermedius	0 0 0 1 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0
Tamias siskiyou	1 1 1 1 0 0	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0
Tamias townsendii	0 0 0 0 0 0	0 1 1 1 1 1	0 0 1 1 0 0	0 0 0 0 0 0
Thomomys mazama	1 1 1 1 0 1	0 0 1 0 0 1	0 0 0 0 0 0	0 1 1 1 0 0
Zapus trinotatus	0 1 0 0 1 0	1 0 0 0 1 0	1 1 1 1 1 1	1 0 0 0 0 0
Carnivores				
Mustela erminea	0 0 1 0 1 1	1 0 0 0 0 0	0 0 1 0 1 0	0 0 0 0 0 1

All six of the insectivorous species observed in this study are believed to derive habitat benefits from down wood (Brown 1985, Carey and Johnson 1995, Gilbert and Allwine 1991). The almost uniform presence of Pacific, Trowbridge's, and vagrant shrews across the 24 stands would imply that these shrews are not limited by CWD. However, studies at the micro-habitat scale suggest otherwise (reviewed in Verts and Carraway 1998). Of the three insectivorous species for which t-tests could be performed *(table 4),* coast mole *(Scapanus orarius)* did not demonstrate differences in CWD volume between capture and non-capture stands, but both the shrew-mole *(Neurotrichus gibbsii)* and the Pacific water shrew *(Sorex bendirii)* were captured on stands where CWD volumes were more than twice that found on non-capture stands. Interestingly, although the shrew-mole and the Pacific water shrew are both thought to favor moist habitats (Gomez and Anthony 1998), they only overlapped on 9 stands while one or the other species was present on 22 of the 24 study stands. These results suggest that for at least some species, down wood likely works in conjunction with other habitat features to influence stand suitability.

Rodents had a wide range in site occurrence, but only two species showed significant differences in CWD volumes between capture and non-capture stands *(table 4).* Western pocket gopher *(Thomomys mazama)* was observed on stands with less down wood, and Pacific jumping mouse *(Zapus trinotatus)* was observed on stands with greater down wood compared with non-capture sites. Neither species is believed to have strong dead wood habitat relationships (Brown 1985, Gilbert and Allwine 1991, Gomez and Anthony 1998); however, little is known of the habitat requirements of the jumping mouse (Verts and Carraway 1998) despite its apparent preference for riparian areas (Gomez and Anthony 1998). In addition, Verts and Carraway (1998) contend that the western pocket gopher does not occupy dense forest areas, but results from this study and others, and confirmed voucher specimens conflict with this claim.

Table 4—*Results of Welch's approximate t-tests for comparing differences in mean coarse woody debris (CWD) volumes (m^3/ha) in stands in the Umpqua National Forest, Oregon, where small terrestrial vertebrate species were and were not located.*

	Located		Not located				
	Stands (n)	CWD	Stands (n)	CWD	t	df	p
Amphibians							
Salamanders							
Ambystoma gracile	21	236	3	325	0.33	2	0.77
Aneides ferreus	9	307	15	211	1.32	21	0.2
Dicamptodon tenebrosus	7	399	17	185	2.14	7	0.07
Ensatina eschscholtzii	23	254	1	94	--	--	--
Plethodon dunni	3	441	21	219	2.97	4	0.04
Plethodon vehiculum	7	419	17	176	2.46	7	0.04
Taricha granulosa	16	304	8	133	2.85	20	0.01
Frogs							
Pseudacris regilla	3	100	21	268	3.42	19	0.003
Rana pretiosa	1	205	23	249	--	--	--
Mammals							
Insectivores							
Neurotrichus gibbsii	21	268	3	101	2.79	8	0.02
Scapanus orarius	13	311	11	172	1.88	20	0.07
Sorex bendirii	10	362	14	166	2.51	13	0.03
Sorex pacificus	24	247	0	--	--	--	--
Sorex trowbridgii	24	247	0	--	--	--	--
Sorex vagrans	23	248	1	219	--	--	--
Rodents							
Arborimus albipes	3	500	21	211	1.54	2	0.26
Arborimus longicaudus	8	324	16	209	1.40	14	0.18
Clethrionomys californicus	24	247	0	--	--	--	--
Microtus oregoni	22	234	2	392	0.89	1	0.54
Microtus richardsoni	5	362	19	217	1.40	5	0.22
Microtus townsendii	7	206	17	264	0.86	21	0.4
Peromyscus maniculatus	24	247	0	--	--	--	--
Phenacomys intermedius	1	186	23	250	--	--	--
Thomomys mazama	10	138	14	326	3.01	15	0.009
Zapus trinotatus	11	359	13	152	2.78	11	0.02

Of the remaining species, four are believed to require down wood in their habitat and four appear little impacted by it (Brown 1985). Three of the four species that use CWD were common across the study sites and their routine occurrence in Oregon forests is well documented (e.g., Carraway and Verts 1985, Doyle 1987, Gomez and Anthony 1998, Rosenberg and others 1994, and reviewed in Verts and Carraway 1998). These include western red-backed vole *(Clethrionomys californicus),* creeping vole *(Microtus oregoni),* and deer mouse *(Peromyscus maniculatus).* The fourth species, white-footed vole *(Arborimus albipes),* is one of the rarest microtines in North America (Voth and others 1983). Although it is captured infrequently in a variety of habitats (reviewed in Verts and Carraway 1998), it appears to closely associate with abundant deciduous vegetation (Gomez and Anthony 1998, McComb and others 1993, Voth and others 1983).

The four rodent species captured that do not appear to associate with dead wood at the stand level include red tree vole *(Arborimus longicaudus),* water vole *(Microtus richardsoni),* Townsend's vole *(M. townsendii)* and heather vole *(Phenacomys intermedius).* Red tree voles are primarily arboreal rodents, water voles inhabit streamsides, Townsend's voles occupy moist environments, and heather vole habitat remains under review (Verts and Carraway 1998). Only one heather vole was captured in this study.

There are a number of potential reasons for the inconsistency of some of the wildlife/CWD relationships observed in this study versus other published works: Type I or Type II errors may occur in the statistical analysis of species associations with down wood; the prospective rather than experimental nature of the study may have produced some false results; sampling method bias may have affected the number of species encountered; stand scale associations may not adequately reflect microhabitat associations; and sampling an incomplete range of all possible down wood conditions may have masked species sensitivities to low CWD levels.

The lack of representation of all possible dead wood conditions in any given study is probably the biggest disadvantage to using mean CWD values to evaluate species relationships with dead wood based on capture/non-capture data. In addition, capture and non-capture site comparisons unite stands with varying amounts of down wood based solely on the encounter of as few as a single individual with no consideration of population size. Because population abundance for dead wood associates likely correlates with amount of dead wood, regression analysis is more suited to express this relationship and also to identify volumes above which populations are no longer served by additional dead wood. The reliability of regression results, however, is significantly influenced by the reliability of the abundance estimate. Regardless, mean dead wood comparisons between capture and non-capture stands or stands of different age, structure, or management history is the most published statistic for animal/dead wood relationships, and it is frequently used to compare results among studies. Included in the scope of the current study, regression analysis was performed with animal abundance data to expand on the CWD mean comparisons, but regression results will be reported elsewhere.

Conclusions

Although some small terrestrial species at the stand scale do not appear to associate with dead wood, current results do not preclude the importance of dead wood as a micro-habitat feature. Amphibian and insectivore richness correlates highly with CWD volume and most likely is linked to the importance of dead wood as a habitat moderator for these species and as a source of insect food items. Because of the tie between small vertebrates and CWD coupled with the noted importance of down wood at the micro-habitat scale for many species, CWD manipulation at the stand scale should have a large impact on the richness of ground dwelling vertebrates.

The CWD volumes examined in the 24 stands of this study were greater than five times the current CWD Federal targets for southwestern Oregon. If the richness trends observed with down wood volume determined in this study extend to the lower Federal target levels of CWD, then terrestrial vertebrate richness is predicted to be lower than richness observed in this study on sites where minimum Federal CWD targets are implemented. To maintain the full component of small vertebrates typical of Pacific Northwest forests, a logical dead wood management strategy would be to provide for heterogeneity in down wood across the landscape representing the full range of natural levels. The challenge, however, will be to determine the natural range of CWD conditions and to provide an ecological rationale for the proportional allocations of different CWD volumes.

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Stag Retention and Use by Arboreal Marsupials in Eucalypt Forests of Southeast Queensland, Australia: Implications for Management[1]

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Abstract

Dead standing trees ("stags" in Australia) are critical for wildlife in forests throughout the world. Dynamics of stag recruitment and retention are an interaction of tree mortality, size, deterioration rate, human intervention, and variables related to the structure and physiognomy of the forest. Historically in Australia and elsewhere, timber management involved the removal of stags and resulted in additional stags being lost to fire and wind at greater rates than under "natural" conditions. The current status of stags and the relative importance of live versus dead trees to arboreal mammals were investigated on permanent inventory plots throughout southeast Queensland, Australia. Hollow development was correlated with rates of wood decay and time since death. Density of hollow-bearing trees was 10.2 ± 0.2 stems per hectare (mean ± SE); approximately 50 percent of the hollow-bearing trees were stags. Proportion of standing dead versus live trees was about 1:30. However, dead versus live tree use by arboreals was difficult to determine. Longevity of all stags was estimated to be 50 to 100 years. Although live hollow-bearing trees are more important to hollow-using wildlife in Australia, stags may provide a significant additional hollow resource in managed stands. Adequate densities and distribution of both live hollow-bearing trees and stags are extremely important to forest wildlife communities in both Australia and North America.

Introduction

Over the last decade, countries around the world have been addressing the issue of ecological sustainable development. In 1992, Australia adopted a National Strategy for Sustainable Development, which promotes using, conserving, and enhancing the community's resources so that ecological processes are maintained (Australian Forestry Council 1992). Since that time legislation has been enacted to further this goal, including comprehensive planning and assessment systems.

The sound use and management of land, water, and native plants and animals is critical to the long-term productivity and profitability of forestry, the health of the environment, and the viability of rural communities. As such, sustainable natural

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resource management is one of the greatest challenges in the new century. Forest managers are continuously faced with the task of limiting pressures on forest resources (e.g., water and timber production, recreation, biodiversity) as human demands and community expectations increase, and the conservation of biodiversity in forests managed for timber is arguably one of the most complex and controversial management issues. In Australia, the National Forest Policy Statement commits governments and industry to develop management systems that cater effectively to the conservation of all indigenous species throughout their natural ranges.

The forests of eastern Australia provide habitat for a wide assemblage of arboreal vertebrates (Ambrose 1982, Lamb and others 1998, Smith and Hume 1984, Smith and Lees 1998, Taylor and Savva 1988). Many of these species make extensive use of tree cavities, or hollows as they are called in Australia, for denning, roosting or nesting, including 42 percent of mammals, 21 percent of birds, and 28 percent of reptiles and amphibians (Ambrose 1982, Saunders and others 1982). Loss of trees with hollows has been identified as the most significant cause of biodiversity reduction in timber production forests of eastern Australia (Lindenmayer and others 1991a, Loyn 1985). Live trees selected to be retained in harvest areas because they contain hollows or future hollows are referred to as hollow-bearing or habitat trees (Lindenmayer and others 1991b). Dead standing trees—called snags in North America and stags in Australia—can also provide hollows for arboreal wildlife and may be selected for retention, but can be expected to decay and fall more rapidly than live hollow-bearing trees (Borsboom 1991a,b; Wormington and Lamb 1999).

This paper is a collation of existing scientific knowledge of hollow use and habitat tree resources in southeast Queensland, Australia, production forests, compiled from a number of studies conducted over many years. We focus on the number and arrangement of habitat trees (including stags) required to support populations of hollow-dependent vertebrate species, particularly arboreal marsupials. Measurements of hollow trees made in permanent inventory plots within the production forests of southeast Queensland have provided baseline information for silvicultural prescriptions that address both sustainable timber production and the habitat requirements of hollow-dependent fauna. Our objectives are to introduce North Americans to the hollow-using terrestrial fauna of eastern Australia, describe the formation of hollows in Australian forests, quantify the abundance of both live hollow-bearing trees and stags, and discuss the relative importance of stags to arboreal marsupials in eucalypt forests of southeast Queensland.

Study Area

Surveys for hollow-bearing trees took place on state-owned forest lands in southeast Queensland, Australia. The major forest type was inland dry sclerophyll at elevations ranging from 50 to 500 meters. Dominant trees were lemon-scented gum *(Corymbia citriodora),* grey gum *(Eucalyptus propinqua),* brown, red, and pink bloodwood *(Corymbia trachyphloia, C. gummifera*, and *C. intermedia),* and broad-leaved red, narrow-leaved red, and grey ironbark *(Eucalyptus fibrosa*, *E. crebra*, and *E. siderophloia).* Sites were often on well-drained soils with level to moderate slopes. Annual rainfall varied between 1 to 2 meters and fell mostly during the warmer months (October-April). Selective tree logging (i.e., harvest of trees above prescribed diameters) and treatment (i.e., killing by ringbarking or poison injection) of decayed and diseased trees were the dominant timber management practices in the region

(Florence and others 1970, Queensland Forest Service 1992). Historically, stags were removed for safety and fire concerns (Crowe and others 1984). These practices, especially the treatment of decayed and diseased trees, are perceived to be the main cause of decrease in numbers of hollow-bearing trees.

Methods

Over the last 50 years, the Queensland Department of Primary Industries, Forestry Division, has established a series of permanent survey plots in native hardwood forests to determine individual tree and forest stand growth rates, as well as other parameters. These plots are located in commercial forests and are managed no differently from the surrounding forest. Periodic measurements (approximately every 5 years) have provided data to calculate periodic annual increment (PAI) of diameter at breast height (DBH); PAI of species can be used to estimate the age of individual trees in the plots. Stand tables and frequency distributions of hollow-bearing live trees and stags were compiled from plot measurement data. Plots were grouped by rainfall, soils, geographical location, species mix, stand productivity, harvesting regime, and silvicultural management history.

In southeast Queensland, 294 permanent plots within 86 state forests, covering a broad range of forest types and totaling 137 ha, were surveyed for habitat trees and arboreal mammals (Ross 1998). We defined a habitat tree as any tree, either alive or dead (i.e., stag), having at least one visible hollow with an entrance diameter >10 centimeters. As many animals use hollows with openings <10 centimeters, our estimate of habitat tree density is conservative. Plots were surveyed for number of live and dead habitat trees. Densities of live and dead habitat trees were calculated from counts on permanent plots, and age was estimated by the PAI and DBH of each tree species. In addition, stags >3 m in height were measured and number of hollows were counted in trees >30 centimeters DBH (Ross 1998). We report means and standard errors for tree and stag densities, measurements, and ages.

At an additional 38 sites in southeast Queensland, surveys for nocturnal arboreal mammals were conducted at night on 1-km transect lines running through permanent plots wherever possible. Twenty of these transects were close to or passed through 20 of the 294 permanent plots. At pre-designated stations, located every 25 meters along transect lines, surveyors waited quietly for about 3 min., and then used a portable spotlight to search the canopy for arboreal marsupials. Living and dead hollow-bearing trees within 30 m of the transect were counted to obtain density of hollow-bearing trees. Other habitat data (e.g., forest type, basal area) were obtained from three 0.25-hectare plots on each transect.[5]

Results

Current Status of Hollow Trees

Of 294 permanent plots surveyed, 242 (82 percent) contained hollow-bearing stems (Ross 1998). Hollow-bearing trees occurred at a mean density of 10.2 ± 0.2 stems per hectare across all forest types, with about 50 percent being stags *(table 1).*

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[5] Unpublished data on file at The University of Queensland, Brisbane, Queensland, Austrialia.

For trees >30 centimeters DBH, 12 percent of live trees and 93 percent of stags had hollows.

Table 1—*Densities (mean ± standard error) of live and dead (i.e., stags) trees >10 centimeters diameter at breast height on permanent plots located on commercial forest lands in southeastern Australia. Habitat trees are any tree having at least one visible hollow with an entrance diameter >10 centimeters in size (adapted from Ross 1998).*

	Live trees	**Stags**	**Total**
Total stems per ha	250[1]	8.2[1]	258.2[1]
Hollow-bearing stems per ha	5.7 ± 0.3	4.4 ± 0.2	10.2 ± 0.2
Habitat trees per ha	2.4 ± 0.2	3.0 ± 0.2	5.5 ± 0.2

[1] Standard error (SE) was not provided by Ross (1998).

The proportion of hollow-bearing stems in a given size class increased with increasing DBH: 4 percent of trees 30-39 centimeters DBH had hollows, whereas 70 percent of trees 40-90 centimeters DBH contained hollows. These larger trees contained many more hollows on average than smaller trees, and many of these hollows had larger entrance diameters. In general, live stems bore an average of 2.2 hollows overall (all hollows), with an average of 1.0 hollow per tree for entrance diameters >10 centimeters (Ross 1998). Stags averaged 2.8 hollows per stem, with 1.4 hollows per stem for entrance diameters >10 centimeters.

Hollow-bearing trees represented 42 species, the majority being eucalypts or closely related genera. Hollow development appeared to be species dependent, with some species developing hollows earlier in life (i.e., those species more prone to limb breakage) (Wormington and Lamb 1999). No difference was found in the rate of hollow development within forest types (Ross 1998). Hollow development was correlated with rates of wood decay and time since death.

The majority of permanent plots were altered by selective logging, where larger merchantable trees were removed, in addition to treatments that removed a small number of "healthy" (i.e., no deformities) trees and killed most older hollow-bearing trees. Thus stocking rates of stags increased with increasing level of disturbance. Undisturbed stands had a mean stag density of 4.4 stems per hectare, but stands with three to four logging and/or treatment events had 7.4 stags per hectare. In essence, stags comprised 27 percent of the total tree hollow compliment in undisturbed stands as compared to 68 percent in intensively managed stands.

Ross (1998) examined 660 standing dead trees in the permanent plots. The majority of deaths (about two-thirds) were attributed to natural causes (e.g., senescence, wind, fire, drought, or lightning) or silvicultural treatment (about one-third), with the density of treated stags correlated positively with treatment. The effect of silvicultural treatment at our 38 survey sites was to lower the total number of hollow-bearing trees from 14 to 6 per hectare and change the ratio of stags to live hollow-bearing trees from 1:4 to 2:1.[5]

Survey of Arboreal Mammals

Six species of arboreal marsupials were detected in the dry sclerophyll forests of southeast Queensland: common brushtail possum *(Trichosurus vulpecula)*, greater glider *(Petauroides volans),* yellow-bellied glider *(Petaurus australis),* sugar glider *(P. breviceps),* squirrel glider *(P. norfolcensis),* and feathertail glider *(Acrobates pygmaeus).* Species diversity and abundance were most dependent upon forest type, but a minimum of four hollow-bearing trees per hectare was also required before all species of arboreal marsupials were detected along a transect at any site. Most sites (22 of 38) contained <2 live hollow-bearing trees per hectare (some contained none), with the majority of hollow-bearing trees being stags. The sites that contained low numbers of live hollow-bearing trees were often the sites with other attributes (e.g., preferred tree species, higher leaf nutrient levels and forest productivity) most suited to arboreal marsupials (i.e., good site characteristics except for low numbers of habitat trees).[5]

Discussion

In Queensland, at least 13 species of arboreal and scansorial mammals, 63 species of birds, 23 species of bats, and 35 species of herptiles may either utilize or be dependent on hollows (Queensland Department of Natural Resources 1998, Smith and Lees 1998). Hollow-dependent fauna are defined as species that rely predominantly (i.e., >50 percent of the time) on tree hollows for shelter, roosting, or nesting at some stage in their life cycle. Three broad guilds of hollow-dependent fauna are recognized in Queensland (Lamb and others 1998). Group 1, which are evenly spaced, territorial species with small or medium daily home ranges and require moderate to high densities (2-12 per hectare) of habitat trees, include mammals such as gliders (*Petaurus* spp. and other genera) and possums (*Pseudocheirus* spp. and *Trichosurus* spp.) and birds such as treecreepers (*Climacteris* spp., *Cormobates leucophaea*), kingfishers (*Todriamphus* spp., *Syma torotoro*), kookaburras (*Dacelo* spp.), rosellas (*Platycercus* spp.), many genera of parrots, and several other species. Group 2 are non-territorial species that breed or roost in clusters and include lorikeets (*Trichoglossus* spp. and others), several additional species of birds, and 28 species of bats. These species require low to high densities of habitat trees, but these trees may be clustered or distributed unevenly. Group 3 are large territorial species with large home ranges, such as cockatoos (*Calyptorhynchus* spp. and others), several species of owl, and the lace monitor *(Varanus varius).* These large-bodied animals require very large trees with very large hollows, but these trees may be at low densities.

Specific information on the hollow requirements for most Australian species is lacking, and only limited empirical data are available on the density and spacing of habitat trees required by hollow-dependent fauna. As a group, the arboreal marsupials have been the most extensively studied. Estimates for numbers of habitat trees required to sustain populations of arboreal hollow-dependent mammals in southeast Queensland are wide ranging (<1-48 per hectare). However, based on our analyses, we recommend an average of five to eight habitat trees per hectare, which is a reasonable general management goal and follows Lamb and others (1998). They recommended 8-12 habitat trees per hectare to maintain natural densities of hollow users, with at least half that (i.e., 4-6 per hectare) providing an appropriate compromise for sustaining populations of hollow-dependent fauna in logged forests, though probably below natural densities.

Eyre (1993) and Eyre and Smith (1997) found that yellow-bellied gliders used only one dead standing tree as a den site, as compared with 44 live habitat trees. In contrast, a site in this study that contained very few live hollow-bearing trees had a high abundance of all six species of arboreal marsupials (common brush-tail possum and greater, yellow-bellied, squirrel, sugar, and feathertail gliders). All species except the feathertail glider were observed to use stags regularly for denning.[5] Silvicultural treatments such as ringbarking or poison injection can increase numbers of stags, as was evidenced on some of our plots that had higher levels of disturbance, but stag longevity is lower than that of live hollow-bearing trees. Thus, the retention of treated stags provided a significant hollow resource in altered areas, but with the caveat that stags are more susceptible to fire, wind, and other disturbances and their longevity is far less than live hollow trees.

Dynamics of natural stag retention is an interaction of tree mortality, stag size, stag deterioration rate, site conditions, and other variables (Cline and others 1980, Raphael and Morrison 1987). In North America, the cavity formation process often involves the activities of primary excavators (woodpeckers, family Picidae) (Conner and others 1976, Mannan and others 1980, Raphael and White 1984). In Australia, however, primary excavator species do not exist, and hollow development in commercially important gum forests is an interaction involving mechanical process (e.g., limb breakage, fire scars), fungal infections, and termite activity (Mackowski 1984, Saunders and others 1982, Wilkes 1982, Wormington and Lamb 1999). The process of hollow formation and the relative importance of live versus standing dead trees is thus a dynamic process dependent on several variables, and differs between Australia and North America, at least with regard to primary cavity excavators. However, Waters and others (1990) reported that nonexcavated hollows (i.e., those formed by limb breakage and decay rather than woodpeckers) were more common in oaks (*Quercus* spp.) than digger pines *(Pinus sabiniana)* in California; hollows in pines were exclusively the work of excavators. Thus, hollow formation in North American hardwoods is probably similar to hollow formation in Australian hardwoods. Nonetheless, adequate densities and distribution of hollow-bearing trees and stags is extremely important to forest wildlife communities on both continents.

One of the challenges in managing stags is determining not only how many stags should be on an area, but in what kinds of distributions (i.e., uniform, scattered, clumped). Different wildlife species not only require different sized stags and hollows, but often different distributions, as noted previously in this discussion. A management program for stags on either continent will be a multifaceted problem, involving a diversity of sizes of stags and hollows distributed across the landscape in a variety of patterns. Clearly, thorough knowledge of the life history requirements for the diversity of species involved is a prerequisite.

The current status of hollow-bearing trees in production forests throughout southeast Queensland is determined largely by past silvicultural management. On our plots, the development and abundance of tree hollows was related to stem size and estimated age. Depending on the species, trees need to reach 145 to >200 years of age to provide adequate hollows, with older trees corresponding to larger hollows (Wormington and Lamb 1999). Recent analyses indicate an overall depletion of the hollow tree resource in native production forests (Ross 1998).

The government of Queensland is required to provide a "Code of Environmental Practice for Native Forest Timber Production," which includes the retention of habitat trees (Lamb and others 1998). The Technical Advisory Group that was assembled to address management issues pertinent to retention of habitat trees in native forests of Queensland acknowledged that stags were more susceptible to fire and wind-throw than live trees, but did recognize the importance of stags to wildlife. The advisory group recommended that stags be retained unless there were compelling safety or fire management reasons to remove them. Not only does this benefit wildlife, but assists in restoring the multiple functions that dead wood provides to forest ecosystems, including associations with invertebrate and fungi diversity and the role dead wood plays in carbon pathways and recycling of nutrients.

Loss of stags is only part of the concern, however. Loss of forest habitat is probably the greatest concern in Queensland. Over 400,000 ha of native forest cover is currently being cleared per annum. In most cases this is for agriculture and urban expansion, but vast areas have been converted to plantations, particularly exotic pines. The problem has been further compounded by fragmentation of forest cover and edge effects, i.e., where remnant forest exists between exotic or native plantations. These edges are often exposed when the plantation is felled, leading to additional loss of stags to wind throw. Also, the remnant areas are burnt quite regularly to protect the commercial plantation, leading to increased loss of stags.

The information we present is incomplete and clearly preliminary concerning the requirements of hollow-dependent fauna in Queensland forests. Silvicultural practices have the potential to remove or destroy hollow-bearing trees, leaving insufficient younger trees to replace the losses and thereby modifying forest microhabitats, possibly to the detriment of hollow-dependent fauna. Many other parameters, such as alteration of forest structure and composition, successional age, and fire regimes can affect the distribution and abundance of habitat trees, particularly stags. In addition, management recommendations for the retention of habitat trees should be in accordance with the assemblage of hollow-dependent fauna expected to occur on a particular site or forest type (as requirements vary among species), and not applied uniformly across the landscape. The maintenance of forest biodiversity, particularly hollow-dependent fauna, must be undertaken as part of an integrated strategy that includes consideration of the full range of wildlife habitat requirements such as the structure and composition of the forest matrix resulting from timber harvesting and other disturbances. Because the process of hollow development takes a considerable period of time (Mackowski 1984, Wormington and Lamb 1999) and hollows are more prevalent and larger in large trees, it is important that long term considerations be made to ensure a perpetual supply of hollow-bearing trees for hollow-dependent fauna (Gibbons and Lindenmayer 1996).

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Importance to Soils and Other Forest Resources

Fire as a Coarse Filter for Snags and Logs[1]

James K. Agee[2]

Abstract

Fire played an important role in maintaining and creating conditions suitable for native flora and fauna in the forests of western North America. Recent coarse filter conservation strategies have advocated creating future landscapes that incorporate historic or natural ranges of variability, including fire regimes. Historic fire regimes were variable across the West, and created quite unique coarse woody debris dynamics in low-, mixed-, and high-severity fire regimes. Moving towards more historic landscape structures will require variable standards for coarse woody debris retention.

Introduction

Fire has been the most pervasive natural disturbance factor across western forest landscapes (Barnes and others 1998), but it did not work independently of other disturbances. Fire has had both local and broad scale effects on the forests of western North America (Agee 1993), but these effects differ considerably by fire regime. For many decades, foresters, ecologists, and others neglected the contribution of dead wood to biodiversity in the forest. In a typical interior West forest, about two-thirds of the birds and up to 90 percent of the small mammals, reptiles, and amphibians utilize dead wood for cover, roosting, or foraging for food (Thomas 1979). The dead wood can be snags (standing dead trees) or logs (dead trees or portions of them lying on the ground).

The concept of ecosystem ranges of variability (Morgan and others 1994) has been suggested as a framework for coarse filter conservation strategies (Hunter 1990). A coarse filter conservation strategy seeks to preserve biological diversity by maintaining a variety of naturally-functioning ecosystems across the landscape. If it is possible to produce or mimic the historic ranges in stand size, composition, and connectivity by forest type on current and future landscapes, then much of the habitat for native flora and fauna might well be present. Mimicking the historic ranges of coarse woody debris should also help these conservation strategies. Fine-filter strategies, such as individual species plans or snag retention, might still be needed, but most species and ecosystem elements should be present if natural ranges in habitat are provided (Haufler and others 1996). Although coarse woody debris is an important structural component of forest ecosystems, managing for maximization of coarse woody debris, or having uniform standards across historically variable landscapes, is a fine-filter strategy that can literally backfire. The use of coarse

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woody debris levels characteristic of historical disturbance regimes is recommended as an alternate system more likely to be sustainable (Edmonds and Marra 1999).

The Historical Fire Regime

Natural disturbances range from benign to severe and can be generated from within or outside of the ecosystem (White 1987). The disturbance effects in either case are due in part to current pattern or structure and to the nature of the disturbance. Disturbance is usually characterized by a combination of factors: type, frequency, variability, magnitude, extent, seasonality, and synergism with other disturbances (White and Pickett 1985). The fire regimes of western forests are usually described in terms of historical fires (defined here as pre-European settlement). They are interpreted much the same way as potential vegetation (Daubenmire 1968), namely what occurred historically and what the trajectories of change may be with or without management (Agee 1993). The effect of Native Americans on fire ignitions is inextricably confounded with lightning ignitions, and the historical fire regime therefore includes native ignitions.

Fire regimes based on fire severity (Agee 1993) are defined by effects on dominant organisms, such as trees, and, although broadly described in three classes, can be disaggregated to the forest type or plant association level if desired. The historical high-severity fire regimes were those in which the effect of a fire was usually a stand replacement event. Fire return intervals were generally 100 or more yrs. The mixed-severity fire regimes had a complex mix of severity levels, with fire return intervals usually 25 to 75 yrs. The low-severity fire regimes were those in which the typical fire was benign to dominant organisms across much of the area it burned, and fire return intervals were generally 5 to 25 yrs. The Interior Columbia Basin Ecosystem Management Project (ICBEMP) has the synonymous fire regimes of lethal, mixed, and nonlethal, respectively (Quigley and others 1996). Because landscape ecology varied widely across the forest landscapes of western North America *(fig. 1)*, coarse-filter conservation strategies, including attention to coarse woody debris, should recognize that variability.

The Low-Severity (Nonlethal) Fire Regimes

Low-severity fire regimes typically had large fires (Wright 1996) but small patch sizes. Fires burned frequently in these forests (Agee 1993), and by regularly consuming fuels, killing small trees, and pruning the boles of residual trees, maintained a relatively fire-resistant landscape. Forests with significant components of ponderosa pine *(Pinus ponderosa* Dougl. ex Laws.) had very small patch sizes, ranging from 0.02 to 0.35 ha (Agee 1998b, Bonnicksen and Stone 1981, Cooper 1960, Morrow 1985, West 1969, White 1985), due to group kill of pines by bark beetles *(Dendroctonus* spp.), or perhaps root disease pockets, and subsequent consumption of the debris by several fires. Because these dead patches were small and limited in extent, patch edge was also limited. Most of the forest was a fairly uniform mosaic of mature tree clusters and grassy understories.

Before getting carried away by the idyllic vision of an equilibrium forest, it is important to note that exceptions did occur, even in ponderosa pine forests. Defoliation by pine butterfly *(Neophasia menapia* [Felder and Felder]) created much larger patches, at least in some areas of south-central Washington (Weaver 1961), and the Black Hills of South Dakota had pine stands that appear to have had less frequent but more severe fires, and much larger patch sizes (Shinneman and Baker 1997). These latter stands are transitional to boreal forest, containing some white spruce *(Picea glauca* [Moench] Voss). Clearly, though, the wide range of studies in low-severity fire regimes support the notion of an equilibrium system, including at least some of the Black Hills (Shinneman and Baker 1997).

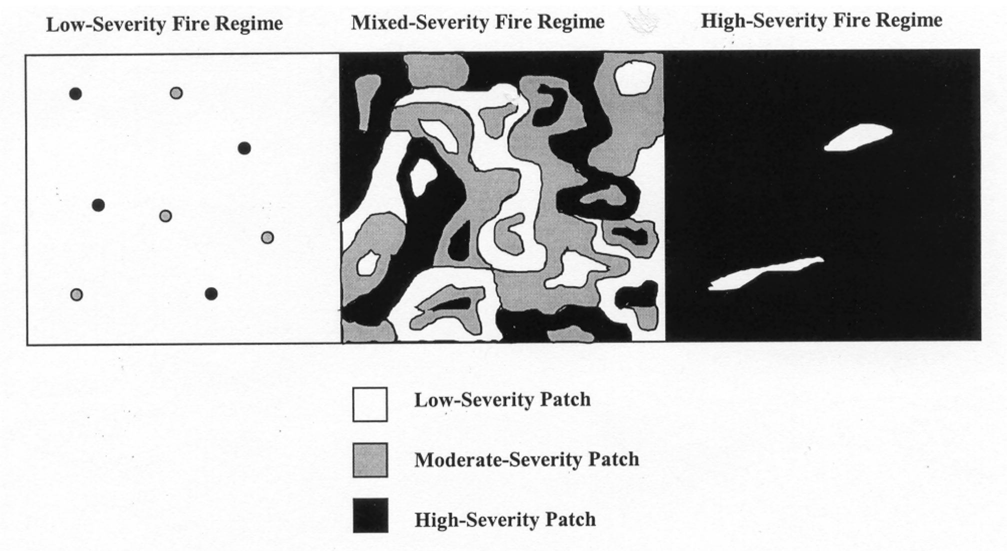

Figure 1—A schematic landscape pattern of fire regimes. Black dots in low-severity fire regimes are very old patches of large, old trees being killed by insects and decomposed by fire, and gray dots are emerging small-sized stands that have less-defined edge with older forest than the recently killed patches. The mixed-severity fire regime is typically a complex mosaic of larger patches of the three fire severity levels, while the high-severity fire regime has large, stand replacement patches (Agee 1998b).

As individual tree clusters became senescent, they would be attacked by bark beetles, creating a patch of coarse woody debris that would be consumed by the next several fires passing under the forest. Coarse woody debris under such a regime, both snags and logs, would have been limited and clustered. Over the landscape was a highly connected system of older forest, dotted with regenerating patches and clusters of coarse woody debris.

For example, a small set of stands in an eastern Cascades mixed-conifer forest might be divided into 16 age classes (patches), each separated from the next by 25 years so that the age range covers 400 years. Each is 0.1 ha in size, and every 25 years, pine beetles attack the oldest stand and group-kill it. Every 10 years fires underburn through the stands. Most thinning occurs when stands are young, so that little substantial snag component is produced except in the beetle-killed patches. Tree density averaged 50 to 60 trees ha^{-1} in historic *Pinus ponderosa* and *Pseudotsuga menziesii* ([Mirb.] Franco) forest series in the eastern Cascades (Agee 1998a, Harrod and others 1999). Therefore, six trees per 0.1 ha were used as the average tree density of an individual patch.

Fires will help to decompose a snag patch by consuming the woody debris, and in this example it will be assumed that after five fire events (50 years) the snags are completely burned down. At any time in this scenario, there is one fresh snag patch (0 to 25 yrs) and one patch in advanced “decay” (25 to 50 yrs). Harrington (1996) found about 80 percent of fire-killed small ponderosa pine fell in less than 10 years; thus, an assumption that a fresh snag patch will have six large, old trees and a decaying patch (25 to 50 yrs) two trees appears reasonable, if perhaps a bit on the high (conservative) side. Therefore, on our landscape of 1.6 ha, composed of sixteen 0.1 ha patches, we have at any one time about eight snags. This is equivalent to 500 snags 100 ha^{-1} (about 200 100 ac^{-1}) and would constitute a sustainable snag density over time in the natural forest. Harrod and others (1998) estimated higher densities of 1,457 to 3,483 100 ha^{-1} (590 to 1,410 100 ac^{-1}) but assumed snags would fall on their own rather than fall being accelerated by fire.

Logs will be a limited resource in this scenario, as they are clustered in the snag patches and the concentration aids ignition and consumption of the logs. Just as the snags were spatially dynamic, logs were as well, but probably had a shorter residence time than the snags because of their proximity to the recurring surface fires. If we assume that the average tree size in the mature clumps was about 75 cm dbh, then snag biomass would have totaled about 8.1 Mg ha^{-1}, and log biomass somewhat less than 5 Mg ha^{-1} for the frequently burned low-severity fire regime.

The Mixed-Severity (Moderate) Fire Regimes

Mixed-severity fire regimes had larger patch sizes and considerable edge *(fig. 1)*. These fires maintained both a naturally fragmented forest structure and fuel structure. Patch size in the mixed-severity fire regimes is typically larger than for the low-severity fire regimes. Patch size for mixed-severity forests (including some drier westside Cascade forests) ranges from 2.5 to 250 ha (Agee 1998b). Patch edge is typically much higher for mixed-severity fire regimes than for high-severity fire regimes (although the methods for defining a patch will significantly influence any edge metric). The result, both from fire and other disturbances, was considerable local-scale patchiness on the landscape (Taylor and Halpern 1991). Patches burned with light fires had surface fuels removed and only understory trees killed. Patches burned with higher intensity fires had some overstory removed (similar to the first entry on a shelterwood) and resulted in a favorable environment for regeneration of a new age class of trees (generally shade-tolerant species: white fir [*Abies concolor* {Gord. and Glend.} Hildebr.] or grand fir [*Abies grandis* {Dougl. ex D. Don} Lindl.], Douglas-fir [on dry sites], red fir [*Abies magnifica* A. Murr.], and/or sugar pine [*Pinus lambertiana* Dougl.]). Patches burned with very high intensity within the mixed-severity fire regime had all the overstory killed and created an environment for shrubfields or new shade-intolerant tree species (typically western larch (*Larix occidentalis* Nutt.) or lodgepole pine (*Pinus contorta* Dougl.) (Antos and Habeck 1981, Cobb 1988). Landscape position in part explains differential severity: lower slope positions had the least amount of severe fire, while upper slopes, particularly of west or south aspect, and ridgetops experienced more severe fire (Taylor and Skinner 1998).

Coarse woody debris dynamics were quite complex in the mixed-severity fire regimes (Agee 1993). Periodic fires consumed log biomass, and in underburned patches, coarse woody debris would decrease. In the patches where either thinning or stand-replacement fire occurred, some log consumption occurred, but snags were also created. A net increase, or pulse, of coarse woody debris was likely after a typical fire event. Decomposition would decrease woody debris loads over time, but replenishment would occur from the periodic fires at 25- to 100-year intervals. Data from Wright (1998) showed for a mixed-severity fire regime in Douglas-fir about 40 Mg ha^{-1} in snags and 55 Mg ha^{-1} in logs, with the totals varying among stands from 20-250 Mg ha^{-1}. Because this fire regime has low-, moderate-, and high-severity patches closely mixed, these levels would probably serve as an integrated average level of coarse woody debris across the variety of patch types and sizes in this fire regime.

The High-Severity (Lethal) Fire Regimes

Disturbance events in high-severity fire regimes often have large patch sizes *(fig. 1).* Although the large majority of fires historically remained quite small, the vast majority of area affected by fire is from the few large events that cover thousands of hectares (Bessie and Johnson 1995, Romme 1982, Romme and Despain 1989). Small fires tend to have little edge, while larger events tend to be more patchy and leave more residual islands (unburned stringers) (Eberhart and Woodard 1987). Generally, the edge created in the high-severity fire regimes is less than in the mixed-severity fire regimes (Agee 1998b).

The distribution of stand ages in the high-severity fire regimes is not clear. Even if an assumption about the nature of disturbance allows a fit of age classes to a distribution such as the Weibull or negative exponential, there are still assumptions about long-term stability (e.g., stable climate over centuries) that may alter the age class structure. Several characteristics of the high-severity fire regimes of western forests are unquestionable: the fire return intervals were long (usually >100 yrs); some stand ages exceed the average fire return interval, suggesting that either the concept of "refugia" (Camp and others 1997) or just random chance are operating; and fires often impose a new landscape mosaic by burning stands of various ages (Bessie and Johnson 1995).

Coarse woody debris dynamics in the high-severity fire regimes typically followed a "boom and bust" cycle (Agee and Huff 1987, Spies and others 1988). After a large fire event, coarse woody debris was at a high, as the live trees were all converted to snags and then logs *(fig. 2).* As the new stand developed, the coarse woody debris levels dropped as the fire-created material slowly decomposed, and snags created by self-thinning of the new stand were too small to add much volume. In mid-succession, perhaps 100 to 200 years, severe thinning by disease and insects could create pulses of coarse woody debris, and as succession proceeded these levels slowly increased by additions of individual trees. Wright (1998), working in high-severity Douglas-fir forests of the Oregon Cascades, showed an average of 150 Mg ha^{-1} in stands generally 200 years post-fire and older. Agee and Huff (1987) showed the variability over a chronosequence in moist western hemlock (*Tsuga heterophylla* [Raf] Sarg) Douglas-fir forest *(table 1).*

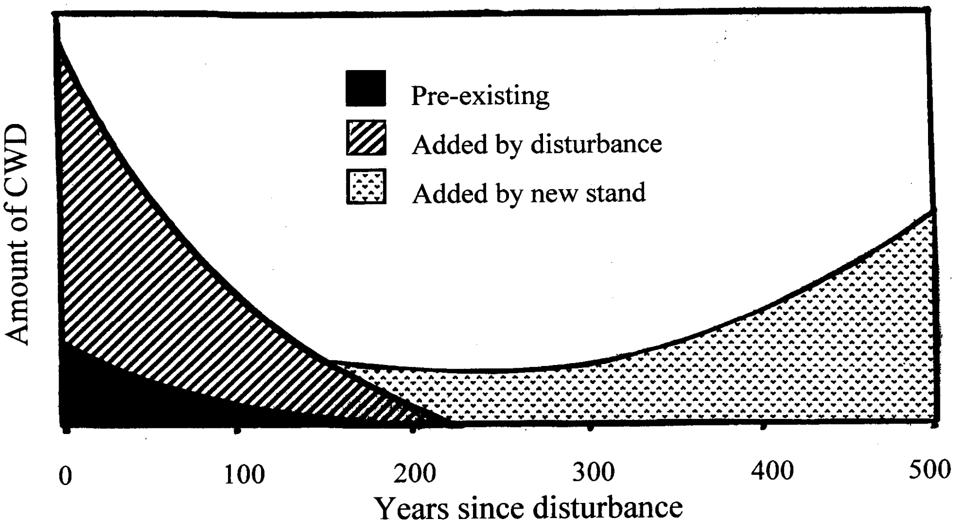

Figure 2—Trends in variation in coarse woody debris loads in high-severity fire regimes in moist western hemlock/Douglas-fir forest, Olympic Mountains, Washington (Agee and Huff 1987).

Table 1—*Coarse woody debris loads over a 500-year chronosequence in western hemlock forest in the Olympic Mountains, Washington (Agee and Huff 1987). This is a high-severity fire regime.*

Type of coarse woody debris	Post-fire stand age (years)					
	1	3	20	100	180	500
	mg ha^{-1}					
Snags	775	1,066	279	35	33	84
Logs	282	230	438	118	112	441
Total	1,057	1,296	717	153	145	525

Coarse Filter Implications

The examples of coarse woody debris dynamics discussed imply quite unique amounts and patterns among the low-, mixed-, and high-severity fire regimes *(fig. 3)*. The low-severity fire regime had quite low biomass with minor fluctuations; the mixed-severity fire regime had higher loads on a sustainable basis but more fluctuation in levels over time; and the high-severity fire regimes had the highest loading, and substantial fluctuation over time. Coarse woody debris standards, if they are to mimic the natural forest, must be designed to fit the forest to which they are applied.

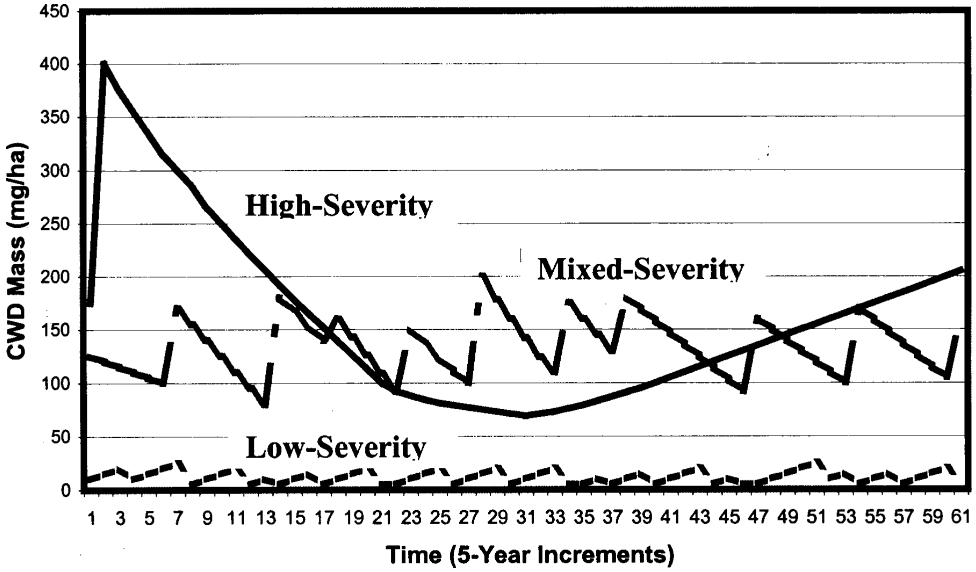

Figure 3—A model of coarse woody debris dynamics in low-severity, mixed-severity, and high-severity fire regimes in western forests. Average amounts of coarse woody debris and fluctuations vary by fire regime.

Natural processes such as fire can be restored to create ecologically sustainable forests (e.g., Dale and others 1999) only if coarse woody debris standards are tailored to the forest type and historic fire regime. For example, in a mixed conifer forest with a historic low-severity fire regime, prescribed fire in either spring or fall *(fig. 4)* will substantially reduce coarse woody debris. Residual coarse woody debris loads in this example were about 40 Mg ha^{-1} (Thomas and Agee 1986), still well above the levels of historic forests with a similar historic fire regime. Burning prescriptions designed to retain most coarse woody debris can produce a "non-window": duff moisture levels so high that such moisture contents are rarely if ever attained on these sites. Constraints to preserve all or most coarse woody debris effectively eliminate the use of fire for restoration purposes and leave the dry forest types at risk for stand-replacing fire. When such high-severity fire occurs, it brings with it the "boom and bust" coarse woody debris dynamics of the high severity fire regimes. This is a classic case of the fine-filter (log preservation) trumping the coarse-filter (restoring the natural process), and in the long run is likely to result in a failed conservation strategy (Agee 1999).

Unfortunately, few coarse-filters can be successful on their own. We can reintroduce the friendly flame, but in many western forests the historic structure is gone: too few large trees, too many little ones, and substantial time before new large coarse woody debris will be produced. Today many species are at the brink of extinction so that natural processes like fire, reintroduced at historic levels in a damaged ecosystem, may be inappropriate. The role of fire as a coarse-filter conservation strategy (Agee 1999) cannot be blindly applied as a "natural" solution; it will have to come in many shapes and sizes. However, understanding the historic role of fire will provide a template for designing appropriate coarse woody debris loads in our western forest landscapes. Levels of coarse woody debris, as well as temporal and spatial variability, need to be addressed.

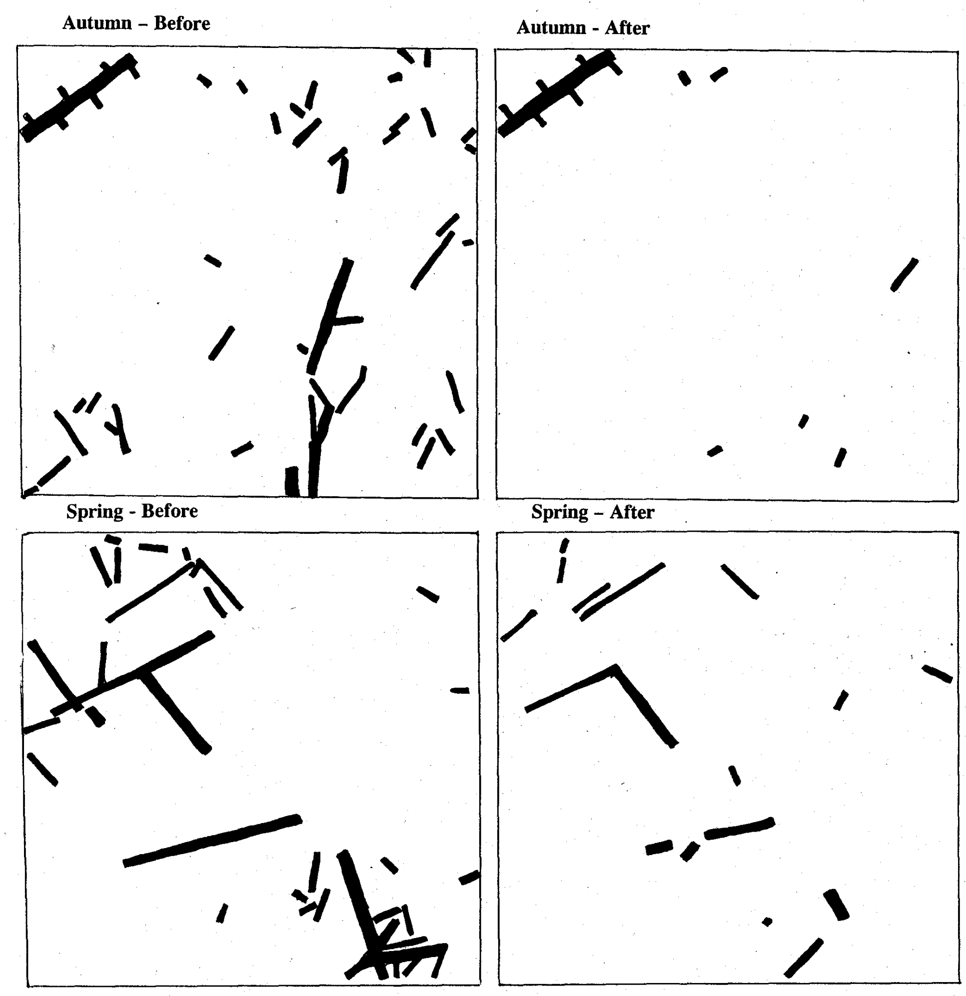

Figure 4—Consumption of logs in spring and autumn burning in mixed-conifer forest of southern Oregon (data used in Thomas and Agee 1986). Plots are 0.25 ha in size (50 x 50 m).

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Assemblages of Vascular Plants on Logs and Stumps within 28-year-old Aspen-dominated Boreal Forests[1]

Philip Lee[2,3] and Kelly Sturgess[2]

Abstract

This study examined the impact of logs and stumps on the understory composition of 28-year-old aspen-dominated boreal forests. Suitable logs covered more than five times the area of stumps in both harvest and wildfire stands. Logs and stumps were colonized by a significantly different assemblage of vascular plants than the forest floor. Initial colonization patterns on dead wood in both wildfire and harvest stands were similar. However, as dead wood decayed, assemblages of vascular plants diverged and became more similar to their respective forest floor assemblages. Regenerating trees and shade tolerant forbs were disproportionately more abundant on logs and stumps, while grasses, shrubs, and shade intolerant forbs were disproportionately more abundant on the forest floor.

Introduction

Treefalls produce a number of different microhabitats (Beatty and Stone 1986). These include root throw pits and mounds, downed boles, stumps, canopy gaps, and leaf and branch piles created from downed canopies. In turn, these microsites create favorable habitats for the establishment of vascular plants by reducing competition with non-vascular and other vascular plants (Harmon and Franklin 1989), facilitating establishment of mycorrhizal relationships (Harvey and others 1987), changing substrate nutrient and moisture conditions (Hale and Pastor 1998), providing suitable physical substrate for establishment of roots (DeLong and others 1997), and increasing light and temperature regimes as with canopy gaps (Canham and others 1990). However, it is unlikely that all plants have an equal ability to utilize these sites. Hence, the differential abilities of plants to colonize sites potentially adds to the spatial and temporal variability within the understory.

In aspen-dominated (*Populus tremuloides* Michx.) boreal forests, treefall microsites may play a significant role in determining the spatial and temporal pattern of understories. Tree falldown rates caused by self-thinning produce elevated densities of logs and stumps. The forest floor coverage of downed logs in

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unharvested stands is relatively high (~10 to 20 percent) compared to other deciduous forests (reviewed in Harmon and others 1986). In turn, the abundance of microsites is potentially an important causal factor in the relatively high diversity of herbaceous and woody-stemmed understory found in boreal forests. Within the boreal forest, the role of stumps and logs as safe sites for tree species has been explored (Cornett and others 1997, DeLong and others 1997, Hornberg and others 1997). Crites and Dale (1998) demonstrated that as logs decay the assemblage of plants shifts from bryophytes to vascular plants.

The overall objective of this study was to examine the contribution to understory heterogeneity created by dead wood on the forest floor. In order to do this we needed to characterize the physical parameters of logs and stumps colonized by vascular plants, measure and project the percent cover of suitable logs and stumps, and compare the composition and relative abundance of species among microsites and forest floor assemblages.

Materials and Methods

Site Description

This study was located in the Marten Hills Forest District, near the town of Slave Lake, Alberta, between 55° and 56° North latitude and 114° and 115° West longitude. We selected four wildfire and four harvest stands from this region. Stands were mesic and dominated (> 80 percent basal area) by trembling aspen, with balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* Moench.), and balsam fir (*Abies balsamea* L.) occurring as secondary tree species.

Selection of the wildfire and harvest stands was based on their close geographical proximity to each other, similar pre-disturbance structure, similar timing of disturbances, and lack of human interference during post-disturbance succession. We used a number of data sources to ensure the wildfire and harvest stands were of similar pre-disturbance composition, age, and post-disturbance succession. All stands were disturbed in 1968. During that year, parts of the Sawridge Hills were subject to a large spring wildfire (> 100,000 ha). Wildfire stands burned as part of that conflagration. Harvest stands were cut during the previous winter as part of regular harvest operations scheduled for that year. These stands did not burn in the subsequent wildfire. Harvest was accomplished by using full tree extraction with conventional feller-buncher and grapple skidder.

Ground measurements, aerial photographs, pre-disturbance timber inventories, and interviews with government and industry personnel confirmed that stands were 110-120 years, aspen-dominated, and had basal areas of ~35 m^2/ha prior to disturbance. Wildfire stands were > 75 ha while harvest stands ranged in size from 35 to 75 ha. To control for disparities in size and shape, all measurements were taken inside of a 50-m buffer from the stand edge. Within each of the stands ten 1-ha plots were randomly established. Within each of these plots, four 50 x 50-m blocks were established.

Field Methods

To sample the suitability of logs for vascular plants, we surveyed 200 to 300 m of line intersects within each stand. On each line a minimum of 200 logs ($\geq$ 5 cm diameter at the point of intersection) were sampled. The vascular plants were identified to species and recorded on each side ($\leq$ 50 cm) of the intersecting line. The diameter and length of log sampled were also recorded.

To estimate the projected area of logs, three randomly placed 25-m transects per plot were surveyed using a line intersect method. We only recorded the most common classes and sizes of logs supporting vascular plants. Only logs from decay classes 5 to 7 and ≥ 20 cm diameter were used in estimations of percent microsite cover. Decay classes 5 to 7 represent progressively more decayed logs (Lee and others 1997). Decay class 5 represents logs with < 50 percent of large wood fragments lost, presence of small decayed blocks, and a deformed trunk outline. Decay class 7 logs have nearly 100 percent humification and no evidence of hard wood.

The suitability and percent cover of stumps was based on walking searches in all plots. The area searched was 100 x 50 m (5,000 m^2). Within each search area, stumps with a top diameter of $\geq$ 4 cm were recorded. Each stump was measured along the longest axis and the bisecting perpendicular axis. An elliptical formula was used to calculate the approximate area covered by each. From these surveys, we developed a "hard" and "soft" classification system for stumps. Hard stumps were visually characterized by a distinct outline with some evidence of hard wood, while soft stumps exhibited a deformed outline and little evidence of hard wood. Soft stumps had characteristics similar to those of decay class 7 logs.

To quantify the percent cover of vascular plants on logs and stumps, we focused on the common decay and diameter classes supporting vascular plants. From a random point within each block, the nearest ($\geq$ 20 cm diameter) logs of decay classes 5, 6, and 7 were selected. A 20 x 20-cm quadrat was randomly placed on the logs and visual percent cover estimates were made for each species of vascular plants. Non-vascular plants were also recorded in broad groups: lichens, mosses, and liverworts. In a similar fashion, the nearest hard and soft stumps were selected from the same point within each block. Stumps had to have a top diameter of $\geq$ 30 cm. A 20 x 20-cm quadrat was placed on the top of the stump, and on the side in each cardinal direction. Percent cover was visually estimated for each species. Estimations on stump sides were based on placement of the quadrat parallel to the stump surface. Forest floor coverages were estimated from quadrats randomly placed at least 2 m from logs or stumps.

Analysis

Comparisons of species per sample and percent forest floor cover were made using an ANOVA with a Standard-Neuman-Kuels post hoc. In all cases, significance differences were set at $P<0.05$. Detrended correspondence analysis (DCA) was the primary ordination technique used to evaluate the relationships between microsites and species assemblages (Hill 1979). The statistical package PCord was used to perform all DCAs (McCune and Mefford 1995). Detrending was accomplished by dividing the first axis into 26 segments. Ninety-five percent confidence ellipses were assigned based on algorithms from the JMP statistical package (Anonymous 1995).

Results

Physical Characteristics

Both the diameter and decay stage of logs and stumps were important factors in determining the degree of colonization by vascular plants. We found that logs and stumps $\geq$ 20 cm diameter captured 95 percent of the colonizing species. In general, smaller diameter logs and stumps were only colonized by small forbs such as *Mitella nuda* L., *Linnaea borealis* L., and *Cornus canadensis* L., whereas larger diameter logs and stumps were colonized not only by forbs but also by shrubs and saplings such as *Salix spp.* L., *P. glauca*, and *B. papyrifera*. Decay class 4 logs and stumps were the earliest stage colonized by vascular plants. However, only two species, *L. borealis* and *Mertensia paniculata* were found on these stumps and logs.

Patterns of Species Richness

The overall species richness of the wildfire and harvest stands was identical: 70 species for each. This indicated that the background number of species available for colonization on dead wood was similar between the stands. Species richness on logs ranged from 21 to 26 species, while stumps varied from 22 to 38 species depending on disturbance type and decay class.

To facilitate comparisons among different microsites, we analyzed the richness data on a per sample basis. Forest floor samples from wildfire and harvest stands exhibited a similar mean species richness of 12.9 and 11.7 per sample, respectively (*table 1*; $P > 0.05$). Species per sample on logs or stumps were lower than those found on the forest floor (*table 1*; $P < 0.05$). In comparisons between wildfires and harvest, four of eight microsite types exhibited more species per sample in the wildfire stand while other microsites exhibited no differences between wildfire and harvest stands.

In both stand types, the number of species per sample increased on greater decay classes of logs and stumps (*table 1*; $P < 0.05$). In wildfire stands, decay of logs from class 5 to 7 increased 4.2 species while decay over the same stages in harvest stands increased only 1.4 species. In wildfire stands, decay from hard to soft stumps increased richness by 1.3 species on the sides and increased richness by 3.2 species on stump tops. In harvest stands, decay from hard to soft stumps increased richness by 3.3 and 3.2 species per sample on stump sides and tops, respectively.

Percent Microsite Cover

In both stand types, percent microsite cover was ordered logs > stumps (ANOVA; df=1, F range 29.9 to 38.9, $P<0.001$; *fig. 1)*. In general, the wildfire stand had a greater percentage of the forest floor covered by suitable dead wood *(fig. 1)*.

Decay and Assemblages

Both logs and stumps exhibited different assemblages of vascular plants than the forest floor of either wildfire or harvest stands. In both stands, decay stages of logs and stumps were spread along the first DCA axis *(fig. 2)*. In general, species assemblages on logs and stumps converged with that of the forest floor as logs and stumps decayed. Decay class 5 logs were the least similar to forest floor samples, while decay class 7 logs were the most similar. Hard stump sides were the least similar to the forest floor while soft tops, hard tops, and soft sides were the most similar.

Table 1—*Mean species per sample quadrat (±1 S.E.) for each type of microsite within 28-year-old wildfire- and harvest-origin aspen-dominated boreal forests.*[1]

Microsite	Wildfire	Harvest
Forest floor*	12.9±0.46	11.7±0.48
Log decay class 5	6.2±0.51^{a}	6.1±0.62^{a}
Log decay class 6	7.7±0.57^{b}	7.0±0.35^{a,b}
Log decay class 7*	10.4±0.64^{c}	7.5±0.37^{b}
Hard stump side*	6.9±0.34^{b}	4.6±0.30^{a}
Hard stump top*	7.2±0.41^{b}	6.7±0.30^{b}
Soft stump side	8.2±0.32^{c}	7.9±0.34^{b,c}
Soft stump top	10.4±0.42^{d}	9.9±0.57^{d}

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[1] Superscript letters denote significant differences within log or stump decay classes ($P < 0.05$). All microsites were significantly less than forest floor sample. Asterisks denote significant differences between wildfire and harvest samples ($P < 0.05$).

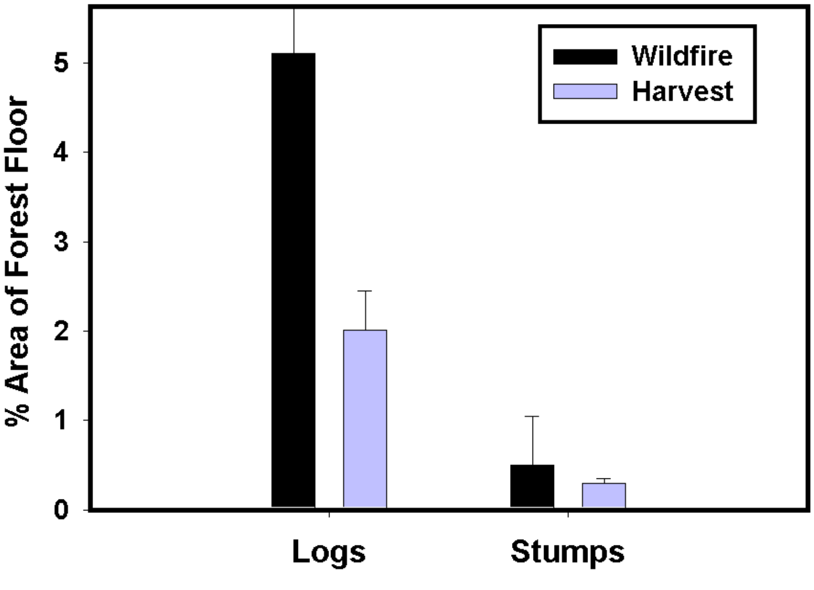
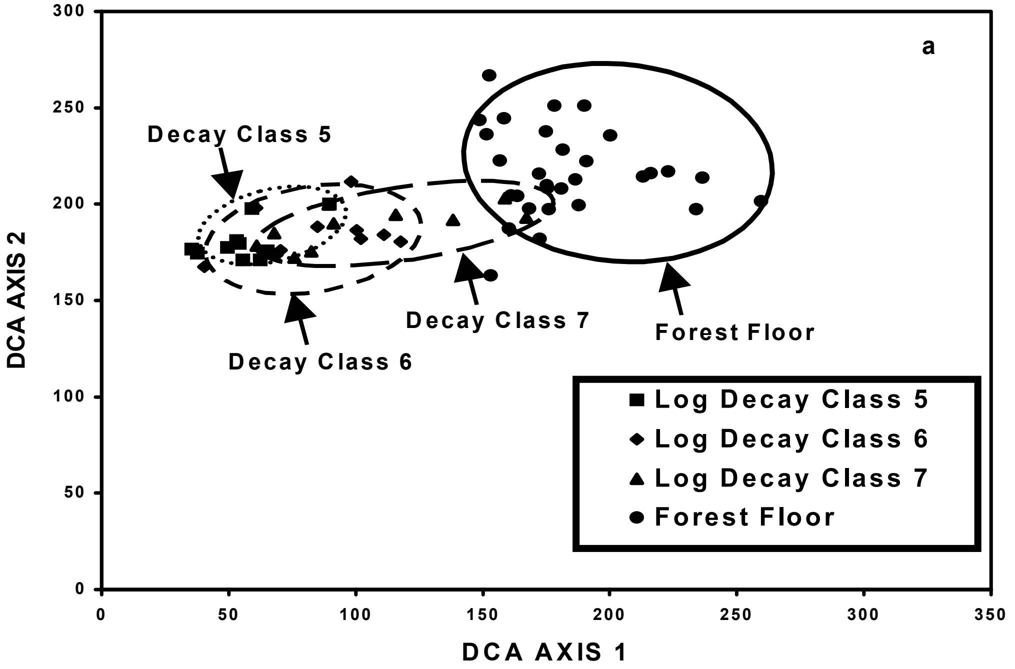
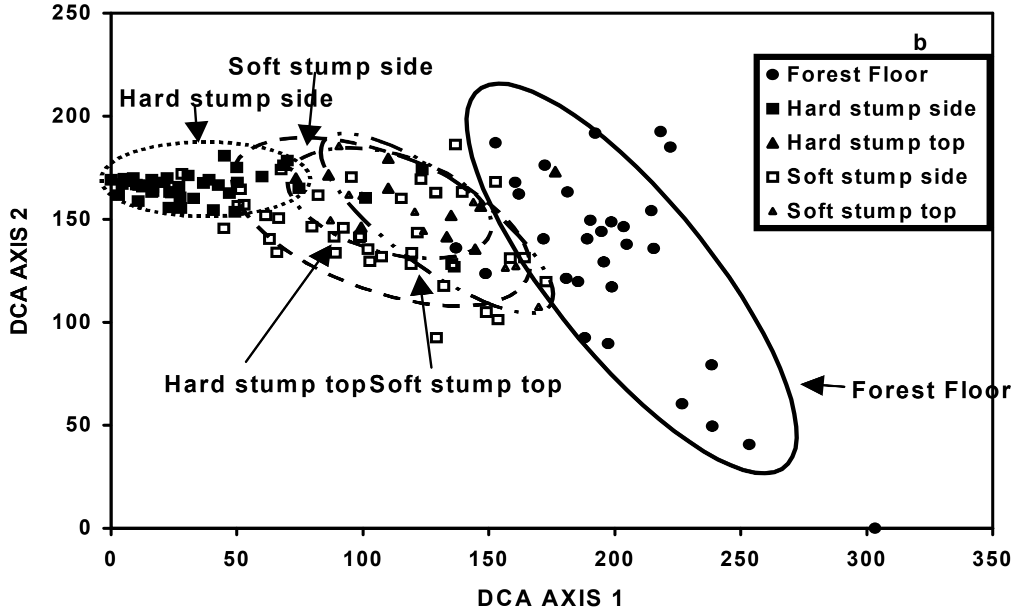


Figure 1—Percentage of the forest floor covered by suitable logs and stumps within aspen-dominated boreal forest.

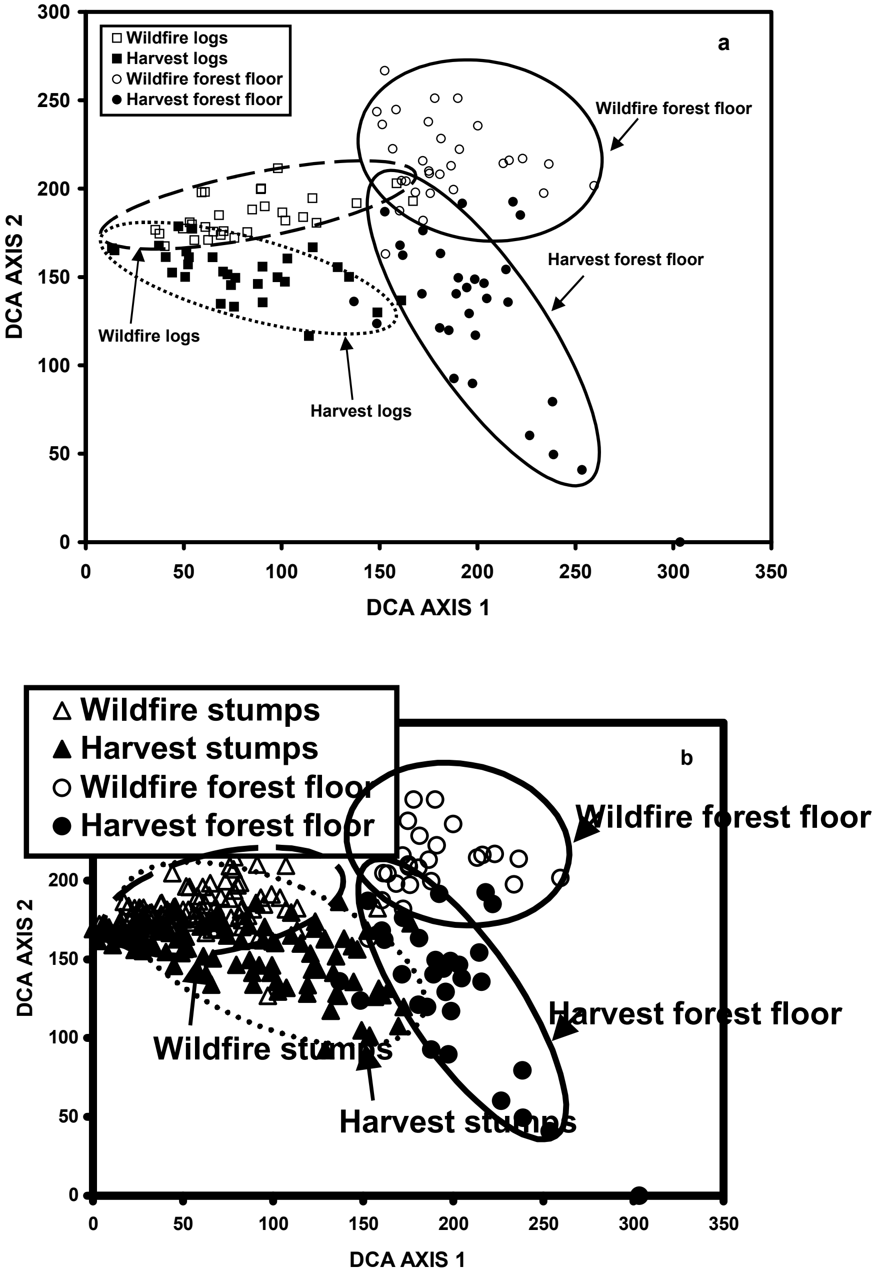




Figures 2—DCA ordination of plot of decay class 5, 6, and 7 logs and forest floor plots from wildfire (a) and plot of hard and soft stumps and forest floor plots from harvest (b) stands. Ordination plots of decayed logs from harvest stands and stumps from wildfire stands exhibit similar patterns but are not shown.

Wildfire and Harvest Assemblages

Assemblages of vascular plants on wildfire and harvest forest floors were different. Most of the variance between disturbance types was partitioned along the second DCA axis *(fig. 3).* Regardless of whether logs or stumps were associated with wildfires or harvests, initial assemblages of plants were similar. As both logs and stumps decayed the assemblages diverged and became more similar to their respective forest floor types.



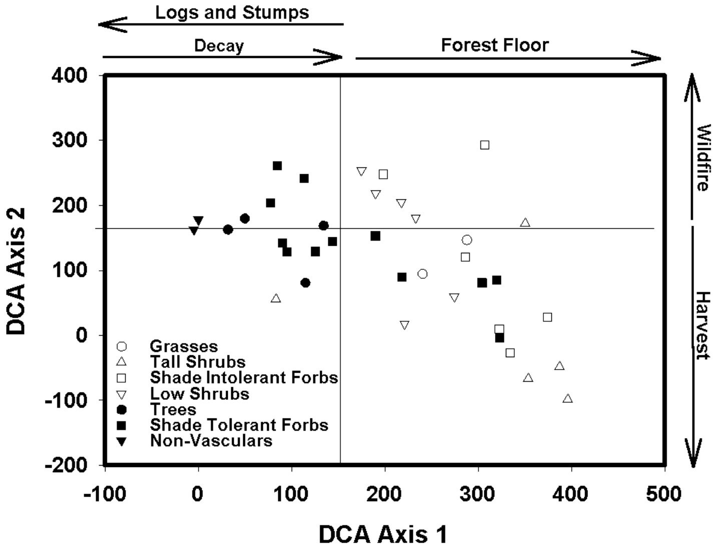
Figures 3—DCA ordination of log and stump plots and forest floor plots from wildfire (a) and harvest (b) stands.

Species Associations

In general, life history and physiognomy of species determined associations with microsites and forest floor sites. To reduce the complexity of plotting and interpreting all species, we classified species with ≥ 1 percent mean cover into the following categories: non-vasculars, grasses, shade tolerant forbs, shade intolerant forbs, low shrubs, tall shrubs, and regenerating trees *(fig. 4)*. Non-vascular plants were classified by broad taxonomic categories, in this case, lichens and mosses.

The ordination plot of species can be crudely divided into four quadrats. Each quadrat represented species associations with particular types of microsites *(fig. 4)*. The right portion of the first DCA axis represents species whose greatest abundance was associated with the forest floor, while the left portion represents species whose greatest abundance was associated with logs or stumps *(fig. 4)*. In a similar manner, the upper portion of the second DCA axis represents species whose greatest abundance was associated with the wildfire stands, while the lower portion suggests an association with harvest stands.

By using this classification, the relationship between species groups and microsites becomes clearer. Lichens and mosses were found on the extreme left of DCA axis 1, indicating dominance in the early stages of log and stump decay. Species groups of vascular plants primarily associated with stumps and logs included some of the shade tolerant forbs and seedlings of the common trees *(fig. 4)*. Seven of the eleven common shade tolerant forbs were associated with logs and stumps. These included *Arailia nudicaulis* L., *C. canadensis*, *Galium triflorum* Michx., *L. borealis*, *M. nuda*, *Rubus pubescens* Raf., and *Trientallis borealis* Raf. Common tree species included *A. balsamifera, B. papyrifera, P. glauca,* and *P. balsamifera.* In contrast, a number of groups were primarily associated with forest floor assemblages. These included the common grasses, shade intolerant herb species, low shrubs, and tall shrubs. One notable exception was *Salix* spp. whose seedlings, like those of regenerating trees, tended to be found on decaying logs and stumps.



Figures 4—DCA ordination of common (≥ 1 percent cover) species categorized by groups: regenerating trees, tall shrubs, low shrubs, shade intolerant forbs, shade tolerant forbs, grasses, and non-vascular plants. See *appendix A* for species within each group.

Discussion

This study demonstrated the importance of logs and stumps in aspen-dominated boreal forests. Our results indicated that logs in advanced stages of decay and stumps were colonized by a significantly different subset of species than the forest floor. Though this study did not track the decay and subsequent colonization of individual microsites, the sequence of decay stages strongly suggested a patterned succession of vascular plants on decaying logs and stumps. As found by McCullough (1948) in spruce forest, we also observed that the domination of lichens and mosses on logs and stumps began to succeed to vascular plants about midway through the decay process. As logs or stumps continued to decay, the assemblage of plants on logs or stumps also changed, eventually becoming more similar to forest floor assemblages. With our two stand types, microsite communities diverged and became more similar to their respective wildfire or harvest forest floor communities.

Changes in the assemblages of plants with decay stage were presumably related to the ability of plants to disperse and establish on logs and stumps through vegetative means, and the ability of both seeds and clones to establish roots. Our first indication of colonization was on decay class 4 logs. This decay class was characterized by the initial breakdown and softening of the log or stump surface. The opening of cracks on the surface allowed for the accumulation of organic matter in cracks and perhaps access to softer heartwood and sapwood in the interior of the log.

In contrast, even hard stumps maintained assemblages of vascular plants. The cracks on the surface and sides of even hard stumps were sufficient to allow the establishment of roots. In part, the relative permanency of stumps, first as part of a living tree, allowed for an accumulation of organic matter within cracks prior to tree death. Aside from being a suitable medium for the germination of seeds and penetration by stolons or rhizomes, both water holding capacity and available nutrients increased with decay (reviewed in Harmon and others 1986). Though the availability of nutrients is less on logs and stumps than on the forest floor, seedlings and clonal plants require less than larger, established plants. In the case of vegetative plants, nutrients may be shunted from ramets on the forest floor to those on the log. In turn, ramets on logs may provide photosynthates and moisture to forest floor ramets.

Aside from decay stage, our results strongly indicated that larger diameter logs accumulated more species than smaller logs. This is not surprising since a wider and taller log provides a greater isolating effect from the influence of the forest floor. Huenneke and Sharitz (1986) demonstrated that logs ($\geq$ 30 cm diameter) were more readily colonized by trees, shrubs and vines in natural and second growth bald cypress-tupelo swamps *(Taxodium distichum-Nyssa aquatica)* than smaller diameter branches (5 cm to 30 cm) or twigs (< 5 cm diameter). In this and other swamp forest systems, larger diameter logs provided a measure of protection against the frequent flooding (Hornberg and others 1997, Titus 1990). Harmon and Franklin (1989) concluded that competition with moss and herbaceous understories on the forest floor was the driving mechanism for the dominance of regeneration of *P. sitchensis* and *T. heterophylla* on logs in Oregon and Washington. Although we have no direct measures for the underlying release mechanisms on logs or stumps, the prevalence of tree seedlings and smaller, shade tolerant forbs suggests that it may be competitive release. Grasses such as *Calamagrotis canadensis* and shrubs were found primarily on the forest floor. Both these groups are highly effective competitors of tree seedlings (Lieffers and Stadt 1994, Place 1965) and possibly of low, shade tolerant forbs.

The percent microsite cover value for the wildfire stand (> 5 percent) in this study is more comparable to conifer rather than other deciduous systems. Harmon (1989) projected a suitable cover of 5.4 percent in *Picea-Tsuga* forests of coastal Oregon and Washington. Takahashi (1994) found projections of 2.6 to 6.0 percent within *Abies-Picea* forests of northern Japan depending upon soil type. In contrast, Thompson (1980) found suitable logs covering only 1.9 percent of an oak-hickory *(Qurecus-Carya)* forest floor in Illinois. The cover for all logs (suitable and unsuitable) in deciduous forests were generally lower (1.6 to 4.0 percent) than in aspens stands (reviewed in Harmon and others 1986).

Our analysis suggested that log, stump, and forest floor assemblages between wildfire and harvest were different. Species associations within harvest stands were comprised of more tall shrubs and shade intolerant forbs. Furthermore, harvest stands exhibited lower coverage of logs and stumps than the wildfire stand. This is largely caused by the absence of a falldown of fire-killed snags as in wildfire stands. Harvest stands exhibited an increased shrub richness and cover, and lower richness and cover of low, shade tolerant herb species. Our results suggest that the lack of logs may, in part, explain this difference in understory communities. A fuller comparison of the role of microsites in producing differences between wildfire and harvest stands would require a larger sample size of stands while controlling or accounting for within-stand variance.

This study has shown the importance of logs and stumps to the understory heterogeneity of aspen-dominated boreal stands. Although this study did not directly measure a temporal sequence, we hypothesize that selective colonization of logs and stumps plays a significant role. The succession of upland boreal forests often features a conversion from early aspen domination to later mixed wood or conifer domination, while understory communities shift from shrub and shade intolerant species to low, shade tolerant forbs (Rowe 1956). Our results suggest that logs and stumps facilitate these successional shifts in the understory and canopy. Further research is needed to fully determine whether the input and decay of logs and stumps, in part, mediates vegetation succession in boreal forests.

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Appendix A—*Species names of the 25 most common species (≥ 1 percent cover) categorized by functional groups.*

Regenerating trees

Populus tremuloides
Betula papyrifera
Populus balsamifera
Picea glauca

Tall shrubs

Salix spp,
Amelanchier alnifolia
Alnus tenuifolia
Alnus crispa
Prunus virginiana

Low shrubs

Viburnum edule
Rosa acicularis
Lonicera involucrata
Rubus idaea
Lonicera dioica
Ribes triste

Shade intolerant forbs

Epilobium angustifolia
Aster ciliolatus
Solidago gigantea
Smilacina stellata
Aster conspicuus
Solidago canadensis

Shade tolerant forbs

Rubus pubescens
Cornus Canadensis
Mitella nuda
Linnaea borealis
Galium trifolium
Maianthemum canadense
Galium boreale
Galeopsis tetrahit
Aralia nudicalis
Mertensia paniculata
Viola Canadensis
Trientalis borealis

Grasses

Elymus innovatus
Calamagrostis canadensis

Non-vasculars

Lichens
Mosses

The Nutritional Significance of Coarse Woody Debris in Three Rocky Mountain Coniferous Forests[1]

Cindy E. Prescott[2] and Raija Laiho[3]

Abstract

The contribution of coarse woody debris (CWD) to carbon, nitrogen, and phosphorus cycles was assessed in forests of lodgepole pine, white spruce-lodgepole pine, and subalpine fir-Engelmann spruce in southwestern Alberta. Mass loss and changes in C, N, and P concentrations in decomposing log segments were measured over a 14-year period. Organic matter input was measured during 10 years for CWD, 1 year for ground vegetation, and 5 years for other aboveground litter types. Carbon, N, and P release from decomposing litter were simulated for a period of 40 years to determine the relative contributions of each aboveground litter type, including CWD. After 14 years, pine log segments had lost 71 percent of their dry mass; spruce and fir lost 38 percent and 40 percent, respectively. The nitrogen (N) content of the logs increased in pine, changed little in spruce, and decreased by almost 30 percent in fir logs. Phosphorus (P) accumulated in decaying log segments of all three species, especially fir logs in which the P content was nearly five times the initial content after 14 years. Tree species with the lowest initial concentration had the greatest relative accumulation. Thus, wood decay organisms may compete with vegetation for limiting nutrients in these forests. The proportion of coarse woody debris (CWD) in aboveground litter input was 19 percent at the pine site, 3 percent at the spruce site, and 24 percent at the fir site. The contribution of CWD to N and P release was 2 percent or less, except at the fir site where CWD released 5 percent of the N. Coarse woody debris does not appear to make a significant contribution to N and P cycling in these forests.

Introduction

The role of coarse woody debris (CWD) as a critical habitat element for many species of organisms is well recognized (Freedman and others 1996), but less is known about the role of CWD in element cycling and productivity of forest ecosystems (Harmon and others 1986). Studies in the coastal forests of the Pacific Northwest, where CWD is particularly abundant and large (Harmon and others 1986, Keenan and others 1993, Sollins and others 1987), have suggested that CWD is an integral component of forest ecosystems, acting as a long term stabilizing storage pool for nutrients. In other coniferous forests, the role of CWD in nutrient cycling has been found to be small (Busse 1994). There is some controversy about the

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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importance of CWD to forest productivity (Fahey 1983, Harmon and others 1986, Spies and others 1988).

Assessing the role of CWD in element cycling requires measurements of the rates of input and decomposition of CWD relative to other litter types. The long time span and considerable temporal variation make it difficult to directly measure CWD input and decomposition. Most previous studies have relied on indirect methods for estimating rates of decomposition and have usually involved chronosequence techniques. Decomposition estimates have usually been based on log inventories by using various backdating techniques (e.g., Brown and others 1998, Sollins and others 1987) that report changes in wood density, as the original mass of the logs was not known (Alban and Pastor 1993, Fahey 1983, Graham and Cromack 1982, Means and others 1985, Sollins and others 1987). In other studies, the mass of CWD was inventoried and rates of decay were estimated with the assumption of constant input (Sollins 1982). These rough estimates may be adequate for management guidelines, but ecosystem models require more precise information on the pattern of mass loss and nutrient release from CWD.

In this study, the rate of CWD input (treefall) was measured for 10 years in three Rocky Mountain forests: a self-thinning lodgepole pine *(Pinus contorta* Loud.) forest, a mature white spruce *(Picea glauca* [Moench] Voss) forest, and an old-growth forest of Engelmann spruce *(Picea engelmannii* Parry ex Engelm.) and subalpine fir *(Abies lasiocarpa* [Hook.] Nutt.). Mass loss and changes in C, N, and P concentrations were measured over a 14-year period in portions of recently fallen logs of the dominant species in each forest (pine, spruce, and fir, respectively). The role of CWD in nutrient cycling in these forests was assessed by determining 1) the proportion of the annual aboveground inputs of C, N, and P that is derived from CWD, and 2) the proportion of the C, N, and P released from aboveground litter that is derived from CWD during a simulated 40-year period.

Study Sites

The study sites were in the Kananaskis Valley in the Front Range of the Rocky Mountains of southwestern Alberta (51°2'N, 115°3'W). Average monthly temperatures range from -10°C in January to 14°C in July. Average annual precipitation is 660 mm, of which 290 mm occurs as snow. Soils are well-drained brunisols overlying primarily limestone glacial deposits. The three study sites were within 5 km of one another in the Lusk Creek basin, adjacent to the Kananaskis Field Station of the University of Calgary. The sites were identified according to the dominant species of overstory tree in the stand, as pine, spruce, or fir (Prescott and others 1989a).

Methods

Wood Decomposition

Standing dead or recently fallen trees approximately 15 cm in diameter of the dominant species at each site were harvested and cut into segments 20 cm long. In September 1984, 70 log segments were placed on the litter surface at 3 m intervals within one 20 x 30 m plot at each site. Unused portions of the harvested logs were used to determine the average moisture content and C, N, and P concentrations—the original dry mass and C, N, and P content of each log segment.

Ten log segments were collected from each site after 2, 6, 10, and 14 years. Logs were cleaned of litter and vegetation, and end pieces were removed. Each piece was weighed fresh, dried at 80°C to constant mass, and weighed. The central pieces were then ground for C, N, and P analyses.

Litter Input

Input of CWD (treefall) was estimated on two 20 x 30 m plots at each site. All fallen trees were marked with paint in August 1984. New (unmarked) downed trees were checked annually for the first 5 years, and once again after another 5-year period. At each time, the species and decay class of each downed tree was recorded and their dbh and length (within the plot) measured. Decay classes were adapted from Triska and Cromack (1979). After calculating the stem volumes, the total dry mass and C, N, and P content of each log was estimated using average density values and nutrient concentrations for each species-decay class combination.

Input of "small woody litter" (i.e., twigs, branches, intact female cones, and bark) was harvested annually for 5 years on ten 3 x 3 m plots at each site. "Nonwoody litter" (i.e. needles, leaves, male cones, female cone scales, and seeds) was collected in fifteen 0.25 m^2 litter traps placed randomly in one 20 x 30 m plot at each site. The traps were emptied at least twice a year for 5 years. Litter input from ground vegetation was estimated during 1985 as described by Prescott and others (1989b). The litter samples were separated into components and dried to constant mass at 80°C.

Carbon, N, and P concentrations were analyzed in five composite samples of each litter type, and used to estimate the mass of nutrients in the annual inputs of each litter type. Samples were ground in a Wiley mill and C concentrations were measured with a Leco carbon analyzer. Nitrogen and P concentrations were analyzed with a Technicon II autoanalyzer after a sulphuric acid-hydrogen peroxide digestion in 360°C (Lowther 1980). Nutrient concentrations were measured only in the original and 14-year logs.

Statistical Analyses

Three equation types were tested to describe the pattern of mass loss from logs over time: linear, exponential and sigmoidal. Linear and exponential equations have been used in earlier studies of wood decomposition, and a sigmoidal curve was suggested by locally weighted regression procedures used for preliminary smoothing of the data. Statistical outliers in the wood decomposition data were identified and excluded from the regression analyses. Nonlinear estimation was done using a Gauss-Newton method and a least squares loss function (SYSTAT 6.0 for Windows 1996).[4] Final equation forms were selected after checking the residuals and assessing the bias of the estimates.

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

Decomposition and Nutrient Release Simulations

To examine the relative importance of the litter types in the nutrient cycles of these forests, organic matter accumulation and annual release of C, N, and P from each litter type were simulated for a period of 40 years. A 1-year time step was used; each year, the mean annual litter input of each litter type was added to the system. Mass loss equations from the log decomposition experiment were used for CWD. Decomposition of other litter types was simulated using the negative exponential decay model (e.g., Olson 1963):

$$\text{Mass remaining at time t / Initial mass} = \exp(-k \bullet \text{t}) \qquad (1)$$

with the decomposition constants (*k*-values) presented in Taylor and others (1991). For materials for which decomposition data were not available, the *k*-value for a material most similar to it was used (e.g., *k*-values for *Epilobium angustifolium* were used for all herbaceous materials). Each litter cohort was progressively decomposed until the mass of the cohort became negligible or the simulation period ended. Organic matter accumulation was then calculated as the sum of the remaining mass of each cohort at each time step, and annual decomposition as the mass lost from each cohort between the time steps. Release of N and P was simplified by assuming nutrients were lost at the same rate as mass.

Results

Wood Decomposition

Mass loss during the 14 years averaged 71 percent in pine logs, 38 percent in spruce logs and 40 percent in fir logs. Carbon concentrations in the decaying log segments changed little during the 14 years, whereas N and P concentrations increased *(table 1).* There was an average net import of 0.78 mg N per g remaining mass in each pine log, and net releases of 0.05 and 0.65 mg N g^{-1} from spruce and fir logs, respectively *(fig. 1).* Phosphorus accumulated in decaying wood of all three species, particularly in fir logs; the amounts of P imported into the logs after 14 years were 0.02, 0.03, and 0.07 mg P g^{-1} in pine, spruce, and fir logs, respectively. For both N and P, the increases in nutrient content during decay were greatest in logs with the lowest initial concentration (pine logs for N and fir logs for P).

Table 1—*Carbon, nitrogen, and phosphorus concentrations of the log segments initially and after 14 years of decomposition.*

Site	Percent C	mg N g^{-1}	mg P g^{-1}
Initial			
Pine	47.76 ± 0.44	0.61 ± 0.12	0.04 ± 0.02
Spruce	49.07 ± 0.82	0.88 ± 0.20	0.03 ± 0.00
Fir	49.76 ± 0.59	1.55 ± 0.35	0.01 ± 0.01
14-year			
Pine	49.77 ± 1.65	2.78 ± 1.08	0.16 ± 0.06
Spruce	50.84 ± 1.08	1.53 ± 0.92	0.08 ± 0.04
Fir	48.44 ± 0.91	2.03 ± 0.94	0.09 ± 0.05

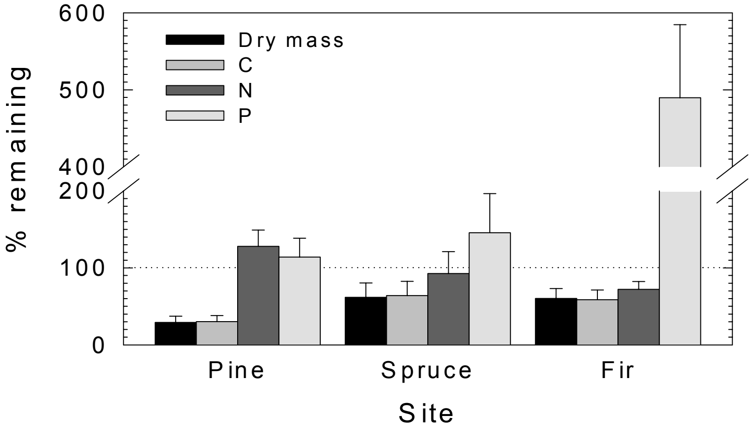

Figure 1—Dry mass, C, N, and P contents of 20-cm log segments of lodgepole pine, white spruce, and subalpine fir after decomposing for 14 years at the pine, spruce, and fir sites, respectively. Values are relative to the initial content: values more than 100 percent indicate net import; values less than 100 percent indicate net release. Each value is the mean of 10 log segments; error bars are one standard deviation.

Litter Input

Total aboveground litter input averaged 362 g m^{-2} $year^{-1}$ at the pine site, 237 g m^{-2} $year^{-1}$ at the spruce site, and 205 g m^{-2} $year^{-1}$ at the fir site. Foliar litter (needles and leaves) made up the greatest proportion of the litter input at all sites *(fig. 2).* CWD input accounted for 19 percent of the litter input at the pine site, 3 percent at the spruce site, and 24 percent at the fir site. For C, the values were 18, 3, and 23 percent, respectively. CWD accounted for 2.6, 0.4, and 5.1 percent of the annual aboveground N input and 1.4, 0.5, and 2.2 percent of the annual aboveground P input at the pine, spruce, and fir sites, respectively.

Decomposition and Nutrient Release Simulations

Nonwoody litter (mostly foliage and cone scales) also dominated release of C, N, and P *(figs. 3-5).* CWD accounted for 18 percent of the total C released from decomposing litter at the pine site, 2 percent at the spruce site, and 20 percent at the fir site. The contribution of CWD to N and P release was 2 percent or less, except at the fir site where CWD released 5 percent of the N.

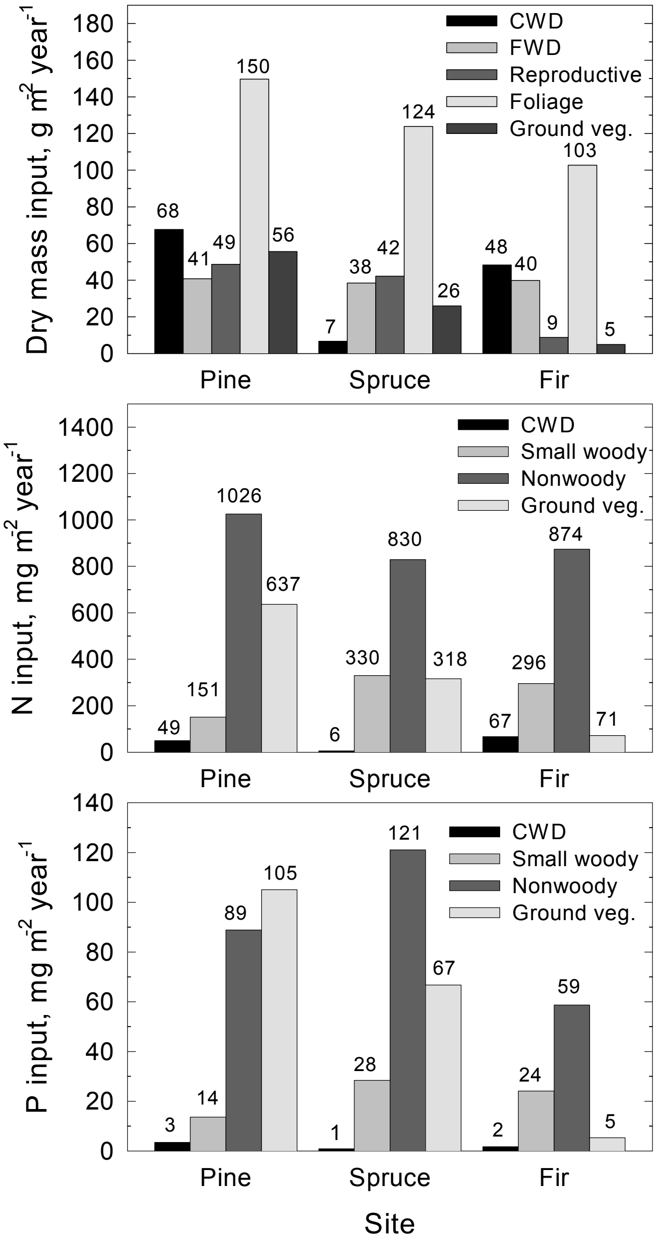

Figure 2—Average annual inputs of dry mass, C, N, and P in each litter type at the pine, spruce and fir sites. CWD = coarse woody debris; FWD = fine woody debris.

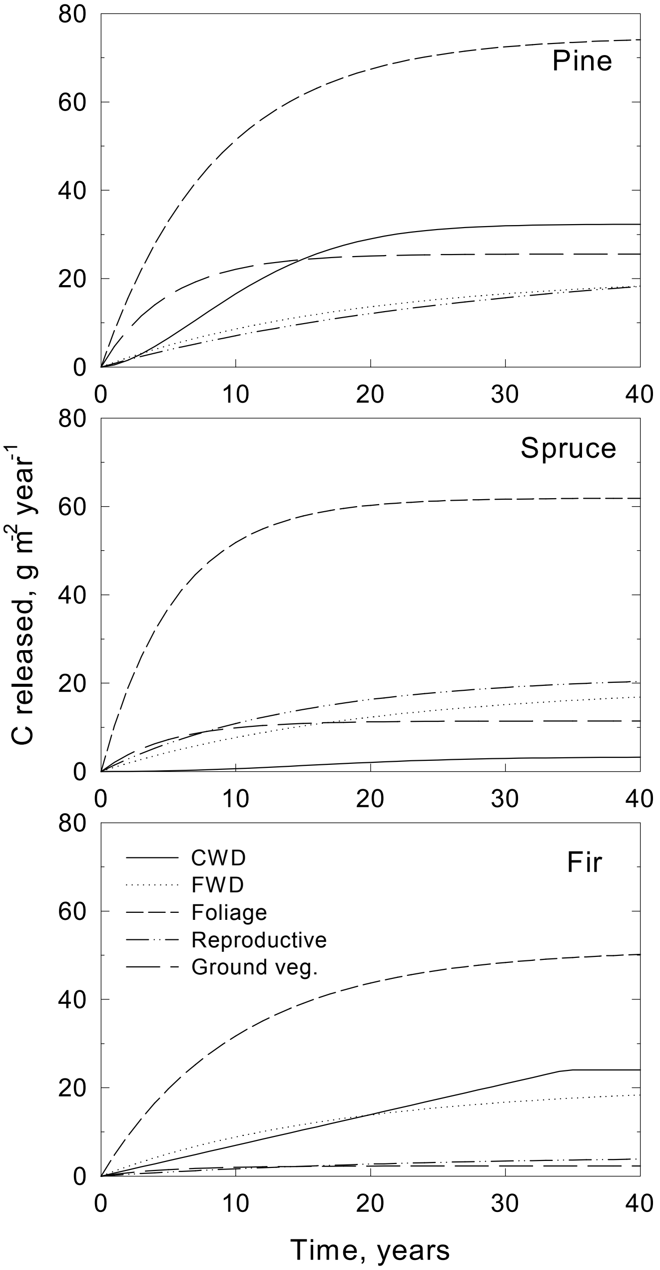

Figure 3—Contributions of the various litter types to annual C release from the accumulated organic matter at the pine, spruce, and fir sites during a 40-year simulation period.

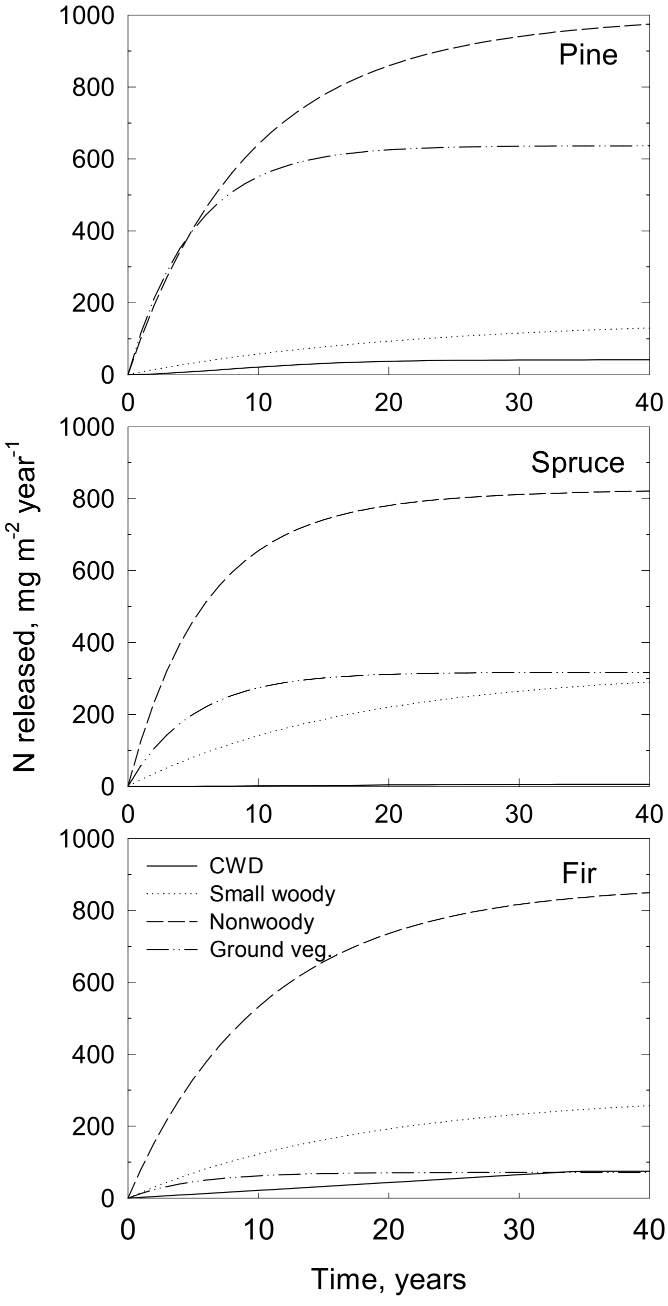

Figure 4—Contributions of the various litter types to annual N release from the accumulated organic matter at the pine, spruce, and fir sites during a 40-year simulation period.

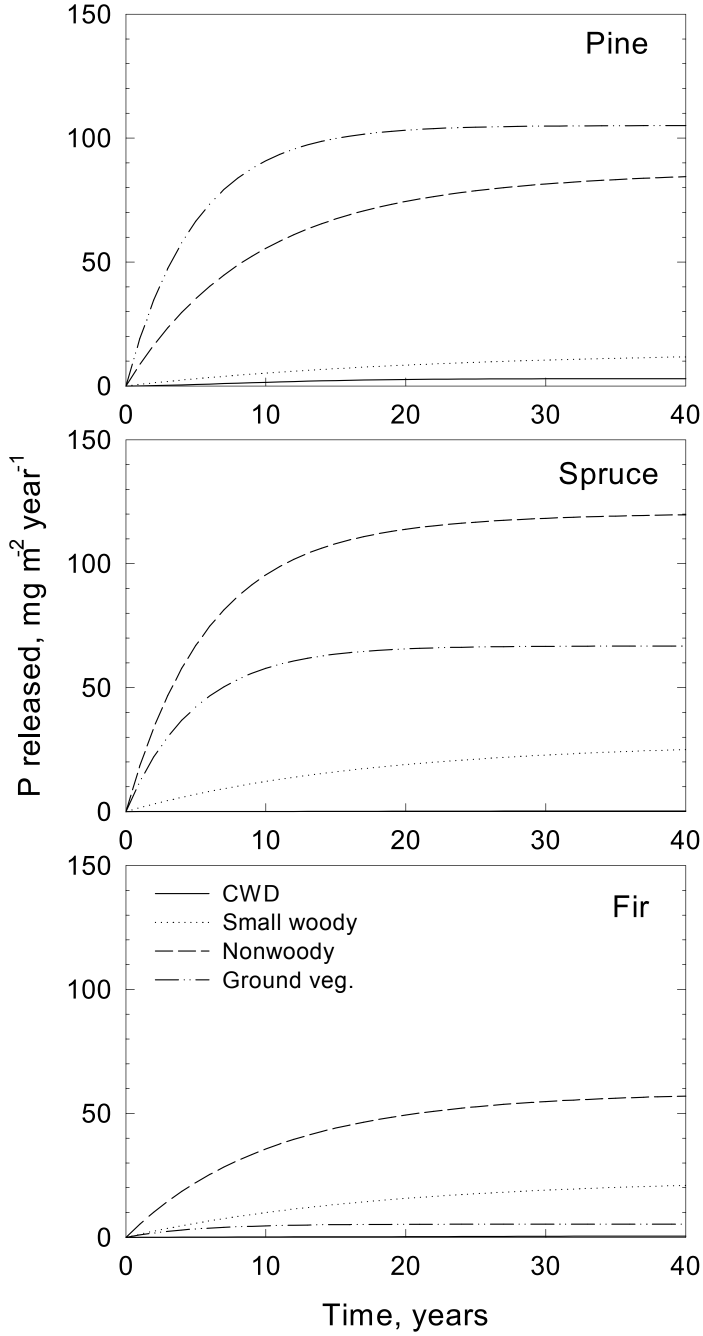

Figure 5—Contributions of the various litter types to annual P release from the accumulated organic matter at the pine, spruce, and fir sites during a 40-year simulation period.

Discussion

Our results indicate that CWD contributed a maximum of 5 percent of the N and P returned in annual aboveground litter and a maximum of 5 percent of the N and P released during decomposition. Other studies have also indicated that the contribution of CWD to nutrient cycling in undisturbed forests is relatively minor. Downed wood comprised less than 3 percent of the soil nutrient pools in lodgepole pine stands in central Oregon (Busse 1994). Fahey and others (1985) found that downed wood accounted for less than 3 percent of the soil N pool in two lodgepole pine ecosystems in Wyoming. In an old-growth mixed conifer forest in central Oregon, well-decayed logs contributed only 4 to 6 percent of annual plant N uptake (Hart 1999).

CWD was clearly more important for the C flows, accounting for 18, 3, and 23 percent of the C returned in aboveground litter, and 18, 2 and 20 percent of the C released during decomposition at the pine, spruce, and fir sites, respectively.

Our observation that logs with the lowest initial concentrations of N or P immobilized the greatest amount of N or P during decomposition has implications as to the role of CWD as a nutrient source in these forests. The initial concentrations of N and P in the logs corresponded to the availability of the nutrient at the site, as determined in previous studies (Prescott and others 1992). For example at the fir site, availability of N was high and P was low, and the logs released N and immobilized P during decomposition. In contrast, N availability was lowest at the pine site, and the logs at this site were the only ones to immobilize N. Release dynamics of N and P in other litter types have been found to depend on the initial concentrations (Prescott and others 1993), and a similar pattern has been noted for decaying wood (Alban and Pastor 1993). Wells and Boddy (1990) and Wells and others (1990) have shown that wood-decaying fungi translocate P from surroundings to the substrate they are colonizing. Our findings of greatest N import into logs at the pine site and greatest P import at the fir site suggest that wood decay organisms may be competing with vegetation for limiting nutrients.

Our estimates are only valid for these forests at the time of measurements, but the sites represent a variety of common forest types and stand development stages: a dense self-thinning lodgepole pine stand, a mature post-thinning spruce stand, and an old-growth spruce-fir stand.

In conclusion, our findings indicate that CWD is not a significant source of available N and P in these forests; it may actually compete with vegetation for limiting nutrients. Guidelines for management of CWD should be based on management objectives related to other potential values, rather than its role in N and P cycling.

Acknowledgments

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The Effects of Microsite (Logs versus Ground Surface) on the Presence of Forest Floor Biota in a Second-growth Hardwood Forest[1]

Charlotte Pyle[2] and Michelle M. Brown[2]

Abstract

A study conducted in forests at the University of Connecticut investigated the value of logs for biodiversity in second-growth hardwoods. Forest floor microsite (log versus featureless ground surface [soil and leaf litter only]) was significant ($P < 0.001$) for the frequency of occurrence of representatives of all seven broadly defined life form groups examined. Algae, non-vascular plants, and fungi were found on logs, but not on the ground. Small mammal and bird perching was noted on logs, but not on the ground. Seedlings and non-seedling vascular plants occurred on both microsites, but were found in significantly greater frequency on the ground surface.

Introduction

Forest floor structure is the result of a variety of natural and anthropogenic processes that create features that persist for a wide variety of time periods. Features resulting from glacial activity (for example, erratic boulders or hard-packed soils underlying ephemeral ponds) are more or less permanent features. The pit and mound topography created when strong winds uproot trees may persist for centuries (Stephens 1956). The bare soil created when a tree is first uprooted is relatively soon covered by new vegetation or leaf litter while the trunks, stumps, and large branches of broken-off or uprooted trees may persist for decades or even centuries. Variation in forest floor structure results in habitat diversity for both plants and animals.

The habitat value of forest floor logs in particular has been recognized for many groups of species, including birds, small mammals, herpetofauna, insects and other invertebrates, vascular plants, non-vascular plants, and fungi (Bull and others 1997, Elton 1966, Harmon and others 1986, Maser and others 1979, McMinn and Crossley 1996, Samuelsson and others 1994). Logs contribute to forest biological diversity by providing animals and plants with substrate, e.g., for feeding, perching, or residence. Organisms that reside on, under, or in logs also may contribute to the diversity of ecological functioning that occurs in forest ecosystems. For example, log-related organisms are involved in nitrogen fixation (Hendrickson 1991, Larsen and others 1978), nutrient cycling (Harmon and others 1994), mycorrhizal fungal associations

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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(Graham and others 1994, Molina and others 1993), and food chains (Maser and Trappe 1984).

Not every study from which the habitat value of logs has been inferred has involved quantitative, controlled comparisons of the value of log microsites versus other forest floor microsites. However, examples of such studies may be found for a variety of species and more broadly-defined life forms, for example, Barnum and others 1992 *(Peromyscus leucopus),* Bratton 1976 (herbaceous plants), Christy and Mack 1984 *(Tsuga heterophylla* [Raf.] Sarg.), Coney and others 1982 (land snails), Harmon and Franklin 1989 (conifer seedlings), Hofgaard 1993 (tree seedlings), Kruys and Jonsson 1999 (moss/liverwort/lichen/fungi), Minore 1972 (conifer [mostly] seedlings), Nakashizuka 1989 (woody plant seedlings), Olszewski 1968 (small mammals), Rambo and Muir 1998 (moss/liverworts), Steel and others 1999 (small mammals), Summers and Uetz 1979 (woodland centipedes), Szewczyk and Szwagrzyk 1996 (tree seedlings), Tallmon and Mills 1994 *(Clethrionomys gapperi),* and Thompson 1980 (herbaceous plants). In some cases, the extent to which logs are important microsites has been shown to be affected by log decay class.

The purpose of the present study was to compare statistically the use of logs to the use of the ground surface in a second-growth, eastern hardwood forest. Our goal was to evaluate the general significance of logs for a broad range of organisms that use logs in other forest cover types. The organisms we considered represented seven life forms: algae, non-vascular plants, fungi, seedlings, non-seedling vascular plants, small mammals, and birds. The specific study objectives were to determine the significance of forest floor microsite (log versus ground surface) for the frequency of occurrence of representatives of the seven broadly-defined life forms; and for logs only, to determine whether the frequency of representatives of each life form is affected by log species and decay class.

Study Area

The study was conducted in the summer of 1996 in forest on the North Eagleville Tract of the University of Connecticut (latitude 41° 48' 30", longitude 72° 17') located in the vicinity of Storrs, Connecticut. The forest, dominated by naturally regenerated, mature, second-growth oak *(Quercus* L.) stands, lies within the central broad-leaved region of the eastern deciduous forest (Duffield 1990). Annual precipitation averages 1,170 mm, spread more or less evenly throughout the year. The average mean January and July temperatures are -3°C and 21°C, respectively, with an average frost-free season of 156 days (Brumbach 1965). Soils in the North Eagleville Tract are primarily fine sandy loams developed from a glacial till derived from schist, gneiss, and granite. The soils are typically very stony with slopes ranging from 3-15 percent. However, soils with poor or very poor drainage as well as steeper (15-35 percent slope) shallow soils are also included within the area sampled (USDA Soil Conservation Service 1966).

Field Procedures

Following the guidelines of Harmon and Sexton (1996), logs were defined as pieces of coarse woody debris (CWD) at least 1.5 m long. Length was measured from the large end to the point where the log diameter tapered off to less than 10 cm. To locate logs for sampling, a line intersect method was used (Ringvall and Ståhl

1999) with randomly located transects laid out within the hardwood forest. Log diameter was measured at the base, mid-point, and upper end of each log intersected by the transect. Each log was identified as "oak" or "non-oak" (Panshin and de Zeeuw 1980) and assigned to one of five hardwood log decay classes (Pyle and Brown 1998). The presence of under-log habitats (leaf litter and soil) was tallied.

Seven broadly defined "life forms" *(table 1)* were chosen to enable quick categorization of organisms into groups that reflected their taxonomy and/or function. We did not explore the relationship of the species included in our life form groups to typical indices of diversity (Swindel and others 1991). For each life form, the presence or absence of any representative species (or, for small mammals and birds, the presence or absence of evidence of perching by any representative species) was tallied for each log. Presence/absence observations of representatives of each life form also were tallied for under-log habitat when it occurred.

Table 1—*Life forms used to categorize the diversity of biota.*

Life form	Description
Algae	Only those visible to the unaided eye
Non-vascular plants	Including mosses, liverworts, lichens
Fungi	Fungal fruiting bodies and hyphae visible to the unaided eye without disturbance of the microsite; and slime molds
Seedlings	Trees $\leq$0.50 m tall; other species with cotyledons
Vascular plants	Excluding seedlings and grass-like plants (Poaceae, Cyperaceae, Juncaceae)
Small mammals	Perching use assessed by presence of scat or nuts/seeds with tooth marks
Birds	Perching use assessed by presence of guano, nests, or proliferations of seeds

The ground surface adjacent to each log was sampled at a distance of 3 meters from the log. For each log, an equivalent area of featureless ground surface (equal to the length times the mid-point diameter of the log) was sampled for the presence/absence of the seven life forms by ground surface substrate (decaying leaf litter and soil). The ground surface samples were taken on alternating sides of the transect and were relocated as needed to avoid forest floor features such as other pieces of CWD or rocks and fine woody debris that might have a different habitat value than leaves and soil.

Data Analysis

For each life form, the significance of microsite type (log versus ground surface) was analyzed using a Haber-corrected chi-square test (Zar 1999) for a 2 x 2 contingency table of microsite type and presence/absence. For each life form, chi-square goodness of fit analysis (Zar 1999) was used to test the significance of log decay class and log species. For decay classes I-IV, the null hypothesis was that the frequency of the j^{th} life form on logs of the i^{th} decay class is proportional to the occurrence of logs in the i^{th} decay class within the sample. With reference to vascular plants, expected values of less than 5 were deemed acceptable for testing extreme departures from a uniform distribution at alpha values of 0.01 because the average expected value (of 7.5 in the case of vascular plants) was at least 4.0 (Zar 1999). For log species (oak or non-oak), a Yates-corrected chi-square goodness of fit (Zar 1999) was applied to the null hypothesis that the frequency of the j^{th} life form on logs of i^{th} species is proportional to the occurrence of logs of the i^{th} species within the sample. The independence of log species and log decay class (for decay classes I-IV) was tested with the log-likelihood ratio (G statistic; Zar 1999). For all statistical tests, *P*-values of less than 0.01 were considered significant. The quadratic mean diameter for the basal end of the logs was calculated as the square root of the average squared diameter.

Results

Two hundred seventy-seven logs and an equal number of adjacent forest floor areas were sampled. The quadratic mean diameter at the basal end of the logs was 31 cm; the median basal diameter was 22 cm. The majority (156) of the 277 logs were decay class II, while 15, 64, 39, and 3 logs were decay classes I, III, IV, and V, respectively *(table 2).* Two hundred nine logs (75 percent) were identified as oak. Nearly half the total sample (46 percent) was class II oak logs *(table 2).* The null hypothesis that log species is independent of decay class was rejected ($P < 0.0001$).

Table 2—*The occurrence of oak and non-oak logs by decay class in the North Eagleville Tract of the forests at the University of Connecticut.*

	Decay class					
Log group	**I**	**II**	**III**	**IV**	**V**	**Total**
Oak	6	128	50	22	3	209
Non-Oak	9	28	14	17	0	68
Total	15	156	64	39	3	277

Strong microsite preferences were found *(table 3).* Algae, non-vascular plants, fungi, and signs of small mammal and bird perching were found on logs, but not on the leaf litter or soil of the adjacent, featureless forest floor. Vascular plants and seedlings were found significantly more frequently on the forest floor samples than on logs. More than 99 percent of the forest floor observations of seedlings and vascular plants involved plants rooted in soil (usually with the roots first going through leaf litter). Under-log habitat also provided shelter for seedlings and to a lesser extent for vascular plants and small mammals *(table 3).*

Seedlings and vascular plants were the only life forms for which decay class was significant ($P < 0.01$). With increasing decay, a larger proportion of the logs in a decay class supported seedlings and vascular plants *(table 4).* Both seedlings and vascular plants occurred in lower (but not significantly lower) proportions than expected on oak logs. This did not alter the trend in the effect of decay class *(table 4).* Log species was not statistically significant for any of the life forms.

Table 3—*The frequency of representatives of seven life forms by forest floor microsite.*[1]

	Microsites				
	Log	Ground surface[2]		Under log[3]	
Life forms		Soil	Leaf litter	Soil	Leaf litter
Algae	218	0	0	0	0
Non-vascular plants	246	0	0	1	0
Fungi	261	0	0	0	0
Seedlings	145	[4]267	1	71	2
Vascular plants	30	[4]265	1	10	0
Birds	17	0	0	0	0
Small mammals	31	0	0	3	0

[1] A total of 277 logs and corresponding areas of ground surface was sampled.

[2] The ground surface sample areas that included seedlings and vascular plants on leaf litter also included these life forms on soil; thus, the tally for ground surface as a whole is equal to the tally for soil.

[3] The under log tallies were neither statistically analyzed alone nor included in the log tallies.

[4] Almost all the seedlings and vascular plants tallied under "soil" grew out of leaf litter but were found to be actually rooted in soil after the leaf litter was moved to inspect the rooting medium.

Table 4—*The proportion of available oak and non-oak logs on which seedlings and vascular plants occurred.*

	Seedlings		Vascular plants	
	Log species group		Log species group	
Decay Class[1]	Oak	Non-Oak	Oak	Non-Oak
I	0.33	0.33	0	0
II	0.41	0.50	0.04	0.14
III	0.54	0.64	0.10	0.14
IV	0.91	0.88	0.32	0.41

[1] Decay class was significant ($P<0.01$) for both seedlings and vascular plants, and log species group was not independent of decay class; however, the differences in occurrence of seedlings and vascular plants by log species group (oak versus non-oak) were not significant.

Discussion

We found a wide range of differences among the seven life forms with regard to the importance of log habitat. We cannot quantify the absolute importance of forest floor logs because we did not quantify the proportions of the forest floor area occupied by logs and by featureless zones. Further, we did not sample all available types of forest floor microsites. Non-vascular plants, for example, were encountered only on logs in our study, but during sampling they were observed to be common on unsampled forest floor microsites, particularly rock surfaces. Similarly, another unsampled microsite, fine woody debris, provides an additional forest floor microsite for algae, non-vascular plants, and fungi in our study area (Kruys and Jonsson 1999).

Forest floor logs and buried wood have been cited as important substrates for tree seedlings in a wide variety of locales, for example, in the Cascade Mountains (Christy and Mack 1984), the Adirondacks (McFee and Stone 1966), and the Great Smoky Mountains (White and others 1985). Our results, which show a lesser importance of logs as habitat for vascular plant seedlings, contrast with these reports.

Some seed characteristics, seedbed conditions, seed sources, and the climatic conditions typical of second-growth, eastern hardwood forests may explain why we found more seedlings and vascular plants on the forest floor than on logs. Our study area is dominated by large- or medium-seeded species, for example oaks and maples. This contrasts with the small-seeded western hemlock *(Tsuga heterophylla* [Raf.] Sarg.) of Christy and Mack (1984), the red spruce *(Picea rubens* Sarg.), Fraser fir *(Abies fraseri* [Pursh] Poir.), and yellow birch *(Betula alleghaniensis* Britt.) studied by White and others (1985), or the studies involving spruce seedlings in Canada cited in support of the notion of foresters' frequently-voiced belief in the significance of decaying trunks and stumps for conifer seedlings (McFee and Stone 1966). Large seeds are less likely to lodge on a log (Szewczyk and Szwagrzyk 1996). The likelihood of seeds lodging on a log is promoted by surficial fissures (Goder 1961), such as those found on large trees, particularly rough-barked conifers. The eastern deciduous forest of North America is typically second-growth where the average overstory tree diameter is much less than that of old-growth forests (particularly those old-growth forests of the moist Pacific Northwest). Further, the microclimate of oak-dominated forests is considerably drier than that of moist coniferous forests. Thus, in comparison to moist old-growth conifer forests, the regeneration of vascular plants on logs in the eastern deciduous forest may be hampered by a combination of a less moist microclimate, larger seeds, and typically smaller logs.

The seedbed conditions provided by logs in second-growth, eastern deciduous forests are less conducive to seedling germination and establishment than the conditions found on the forest floor or on logs in other locales. Seedling germination and establishment on logs requires moisture that may be provided by duff collected on the log surface (Goder 1961) or by decayed wood. The leaves of broad-leaved, deciduous forest trees are much less likely to remain on top of logs to decay into duff than are leaves of small-needled conifers, such as hemlock, spruce, or fir. Further, in our study area (and elsewhere in the eastern deciduous forest), the pool of available logs is dominated by a cohort of hard-surfaced, decay class II oaks believed to be the result of widespread mortality related to heavy infestations by the introduced gypsy moth *(Lymantria dispar* L.).[3] In addition, on the forest floor of oak-dominated forests, there is little competition from moss or herbaceous plants compared to

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[3] Unpublished data on file, C. Pyle, Storrs, Connecticut.

conditions found in other forest cover types (Harmon and Franklin 1989). Thus, even where seedlings on logs are quite numerous (e.g., in canopy gaps), forest floor seedlings also are likely to be equally or more numerous.

Although oak seed source is plentiful, the presence of oak seedlings on logs is largely curtailed by factors that affect seedling placement and establishment. Squirrels bury acorns in soil rather than in logs. Further, the establishment of oak seedlings depends upon the development of a tap root (unlikely to be successful on logs in the early stages of log decay).

Despite these reasons for logs as likely to provide less suitable habitat than that found on the forest floor, some logs in our study area did support the growth of seedlings and vascular plants. We did not tally seedlings by species, but we did observe that in the vicinity of the occasional eastern hemlock *(Tsuga canadenis* [L.] Carr.) trees, certain logs had high concentrations of hemlock seedlings. In areas where the forest floor is covered by a thick layer of oak-dominated litter, the roots of newly germinated hemlock seedlings are unable to send roots through the forest floor litter to the soil. Eastern hemlock regeneration is typically restricted to CWD except where the forest floor has been disturbed (by mixing of organic and mineral soil or by fire) to expose a "partially decomposed layer" (Godman and Lancaster 1990). We speculate that in oak-dominated forests, logs may be found to be more important than the featureless forest floor for the regeneration of other small-seeded species in addition to hemlock.

Our results corroborate the importance of logs for small mammals and birds. Because we used evidence of log use *(table 1),* rather than field sightings of small mammals and birds, our results for these two life forms address the habitat quality of logs only in the context of their preferred use as perches.

Small mammals, seedlings, and vascular plants were observed under, as well as on, logs. Because not every log had habitat under it, our observations of the occurrences of organisms in this type of habitat *(table 3)* were not included in the statistical analysis of log use. However, the deterrent to browsing provided by logs situated above seedlings (Graham and others 1992) may be noteworthy in Connecticut and other locales where ungulate browsing is extensive.

Log decay class was less frequently significant than expected. The state of log decay previously has been found to be important for a great variety of organisms (Crites and Dale 1998, Goder 1961, Hofgaard 1993, Kruys and others 1999, McCullough 1948, Muhle and LeBlanc 1975, Rambo and Muir 1998, Seastedt and others 1989, Szewczyk and Szwagrzyk 1996, Tallmon and Mills 1994). Stronger relationships to decay class might have been found had we used less broadly defined groups of organisms. Finally, it is worth considering that there are multiple decay classes present within most logs of a given decay class classification (Pyle and Brown 1999). In our study, the degree of habitat differences among logs of different decay classes may have been obscured with the tallying of presence/absence, rather than percent cover estimations for life forms, such as algae, fungi, and non-vascular plants.

In contrast to other features of the forest floor (such as rock surfaces and fine woody debris), logs are a relatively long-lasting substrate that may be subject to control through forest management activities. The number, the decay class distribution, and the size of forest floor logs may be strongly influenced by management decisions in commodity forests. As knowledge increases concerning the effects of log-related habitat on biological diversity, managers will be better prepared to make decisions concerning the desired characteristics of the woody debris to be left on the forest floor in logged areas.

Summary and Conclusions

Forest floor logs are an important and manageable habitat component for the promotion of biological diversity. In our study of the frequency of occurrence of seven broadly-defined forms of life on logs as compared to the featureless forest floor, logs were found to be better habitat for non-vascular plants, fungi, and algae, and preferred for perching by small mammals and birds. Further study is needed to quantify the importance of other forest floor features and the importance of the various microsites relative to the proportion of the forest floor they occupy.

Although the frequency of logs with an observed presence of vascular plants and seedlings was significantly less than that for corresponding areas of ground surface, some seedlings and vascular plants did occur on logs in the second-growth hardwood forest study area. The presence of seedlings and vascular plants on logs was independent of log species (oak vs. non-oak), but not of decay class. The more decayed a log, the greater the likelihood that seedlings and vascular plants were present.

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Demographics and Dynamics of Dead Wood

Overview of Agents and Patterns of Mortality and Resulting Coarse Woody Debris Recruitment in Western Forests[1]

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Abstract

We present an overview of many of the mortality agents in western coniferous forests of the United States that are responsible for coarse woody debris recruitment under natural conditions. Patterns and scale of occurrence of mortality agents for the six western USDA Forest Service Regions are examined at both historic and projected-risk time periods. The data indicates that bark beetles have been the most important source of mortality in the western U.S., and with the exception of the Northern Region, this trend is expected to continue. Defoliators, although important in growth loss, have not had as large a mortality impact. Recent-past and projected-risk data indicate that root disease may be an even more important factor in tree mortality and recruitment of coarse woody debris than indicated in recent literature. Although regional measures of actual mortality are not available, all western Regions show high impacts by dwarf mistletoe (*Arceuthobium* spp.) during the past 20 years. Fire affects relatively few hectares compared to insect and disease, but the effects on coarse woody debris (recruitment and conditioning) are important. Additional concerns for managers wishing to augment coarse woody debris are also presented.

Introduction

Coarse woody debris, both standing and fallen, is an important component in many physical, chemical, and biological processes of forested ecosystems (Graham and others 1994). Important functions include erosion control, nutrient cycling, and wildlife and microbial habitat (Harmon and others 1986, Li and Crawford 1994, Light and Burbridge 1985, Lofroth 1998, McGregor 1985b). The role of dead wood in these functions depends largely on such characteristics as size and form, orientation (standing or down), and resident flora and fauna. These characteristics, in turn, are formed by a number of environmental factors including habitat type, forest structure, site quality, climate, geography, disturbance agents, and decay organisms (Harmon and others 1986). Many of these environmental factors are integral to the ecosystem in which the dead wood is found. In other words, the forces that define what may be called a dead wood regime also comprise many of the processes that define ecosystems and communities (biologically delineated zones).

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Dead wood regimes are processes of intermediate time and spatial scales, and interrelated to disturbance and environmental processes, suggesting that analysis of dead wood in the western United States should be done by regions definable by such characteristics as forest type, geography, disturbance regimes, climate, and history; for time frames somewhere between seasonal and geologic; and by including aspects of the various processes in a dead wood regime, such as tree growth, method of death, decomposition and decay. If one process of a dead wood regime is to be used for analysis, disturbance or mortality agents are obvious choices.

The agent responsible for dead wood recruitment often acts on conditions of the live tree (Wargo 1995). These characteristics of the live tree, together with the unique attributes of the killing agent, determine much of the functional pathway followed by the wood in the ecosystem as it deteriorates (Bull and others 1997, Castello and others 1995, Geils and others 1995, Hadfield and Magelssen 1999). Impacts on characteristics of the living tree, either directly on the disturbance agent or on any part of the "death" processes, could change the disturbance process.

Changes in primary mortality agents over time or space could alter the character and distribution of dead wood in the system. Such changes could have important effects on many ecosystem processes (Graham and others 1994, Hagle and others 1995, Harmon and others 1986, Light and Burbridge 1985), and recognition of these changes would constitute valuable information for forest health management. For example, insect outbreaks, fire history, and rangeland condition in the Southwest can be directly related to changes in climate disturbances (Swetnam and Baisan 1994, Swetnam and Betancourt 1998, Swetnam and Lynch 1993).

Our analysis presents an overview of many of the mortality agents in western coniferous forests of the U.S. that are responsible for mortality and subsequent recruitment of coarse woody debris under natural conditions. Spatial and temporal differences in the importance of these agents are examined. Implications of these differences on the ecosystem, on management of coarse woody debris, and on forest health in general are discussed. Finally, risks associated with management activities designed to create coarse woody debris and their mitigation are summarized.

Material and Methods

Analysis Area

Data on the impact of mortality agents was gathered for western coniferous forests of the U.S. Most information was obtained from the USDA Forest Service, in particular, Forest Health Protection. Thus, discussion of patterns and scale of mortality agents will be presented by Forest Service Regions *(fig. 1)*. Because there is relatively little hardwood area in the West, data on forest health in western forests is largely data for coniferous species (USDA Forest Service 1958).

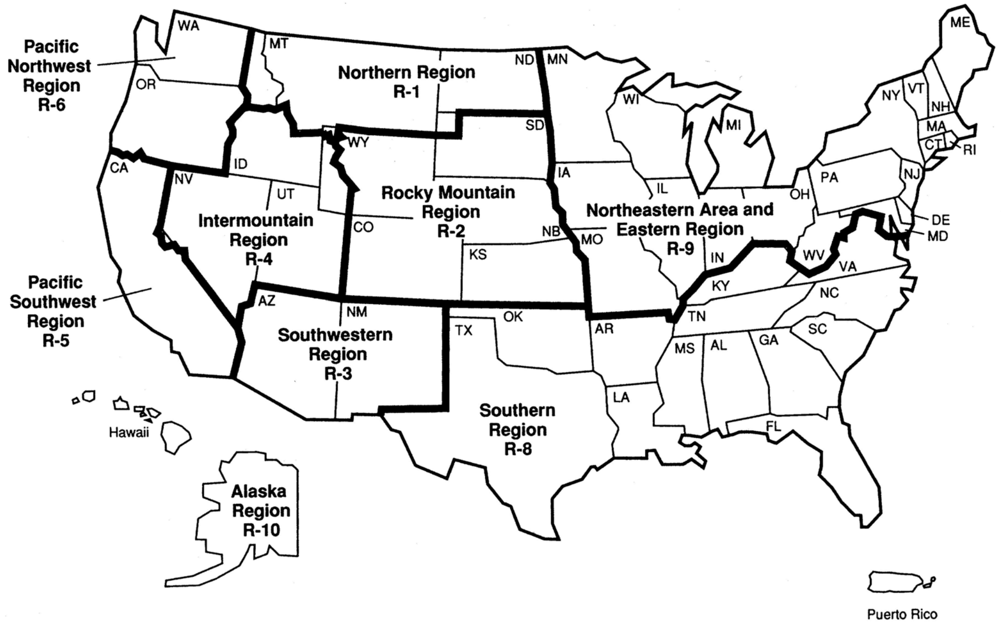

Figure 1—State boundaries and USDA Forest Service Regions.

Patterns and Scale of Occurrence of Mortality Agents

Studies in landscape ecology note that disturbance agents may operate at different spatial and temporal scales and are interrelated (Eng 1998, Harmon and others 1986, Holling 1992, Parminter 1998, Swetnam and Lynch 1993, White and others 1999). The most commonly recognized spatial scales include gap, stand, watershed, and landscape, while common temporal scales include seasonal, annual, and long term. These scales are intermediate in nature between the smallest, fastest, vegetation-directed scale and the largest, slowest, geologic, or evolutionary scale. Because activity at one level both influences the next higher level and contains all the levels found below it (Harmon and others 1986, Parminter 1998), our analysis of the effects of mortality agents on coarse woody debris could be done at many levels (Holling 1992). Ideally, the scale used to evaluate a process should be helpful in the explanation of observable patterns (Eng 1998). However, the availability and the scale (temporal and spatial) of that data may dictate at least the first steps in determining what sizes and time frames are considered.

In our analysis, we chose to review the entire western U.S. Thus, we were limited to a landscape spatial scale of Forest Service Regions and three long-term (approximately 15-20 years) temporal periods: up to and including 1952 (past), 1978-97 (recent past), and 2000-2015 (future based on projected risk). The availability of data for these temporal periods did differ, and in some cases the evaluation of the effects of some mortality agents was not possible. Also, the use of the geo-political Forest Service Region boundaries complicated analysis that ideally should have been related to biologically delineated boundaries.

Measurement of an agent's impact (severity and extent) also was limited. Total area affected was used as the measure for the recent-past and projected-risk data. However, volume measures were used in the 1952 data. The relationship of area affected to the volume of coarse woody debris or number of trees killed has not been determined, and no measure of dispersion (density and patchiness) is available. However, all three measures of impact (area affected, tree volume, stem number), as well as spatial and temporal scales and dispersion, are likely important in assessing the relative effects of any one agent on the ecosystem.

Specific Mortality Agents: Patterns and Scale

Historical (Recent past)—Recent data was compiled for five specific mortality agents for the 20-year period of 1978 to 1997 (recent past). The mortality agents chosen, based on overall importance and data availability, included mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins), western spruce budworm (WSBW) (*Choristoneura occidentalis* Freeman), root disease (RD) (most likely *Armillaria* spp., *Phellinus weirri* Gilbertson, *Heterobasidion annosum* Bref., *Phaeolus schweinitzii* Pat., and *Ceratocystis* spp.), dwarf mistletoe (DM) (*Arceuthobium* spp.), and wildfire (FIRE). MPB was chosen as a principal bark beetle and WSBW as a principal defoliator.

Because of the nature of the mortality agent (slow or fast acting over a large or small area), the data available on the effects of these agents varied. For the insect pests and fire, data generally consisted of annual hectares affected, although the number of trees killed and volume killed were sometimes calculated. Information in national and many regional annual *Forest Insect and Disease Conditions Reports* (issued by the Forest Service's Forest Health Protection) was used to determine annual impacts (hectares) and calculate an annual average impact (total hectares/years) for the six Forest Service Regions and the West as a whole, and to evaluate discrepancies in reported numbers (Bridgwater 1985, DeNitto 1985, Johnson and Hawksworth 1985, McGregor 1985a). In the case of MPB, adequate data was not available for 1978 or 1984. For FIRE, national records were not available until 1984 (USDA Forest Service 1992, USDA Forest Service 1998), although longer fire histories have been reconstructed for areas such as the Southwestern Region by using tree ring data (Swetnam and Betancourt 1998)

Records of annual mortality for RD and DM are not readily available. Aerial detection of these diseases is more difficult and their impact is more gradual, creating problems in making annual mortality calculations. However, average annual impacts of these two agents were evaluated in the early 1980s by the Forest Service. Numbers from these studies and an updated summary of forest health conditions were used in our analysis (DeNitto 1985, Drummond 1982, Johnson and Hawksworth 1985, Smith 1984). RD mortality was estimated as the average annual volume killed (cubic meters) (Smith 1984). Estimates of effects of DM mortality were not available. Rather, volume loss (mortality plus growth loss) was given in both cubic meters and hectares of infestation (Drummond 1982).

In order to display RD mortality on a graph in terms of "number of hectares affected," a ratio was calculated using the available cubic meter measurement of RD from Smith (1984), and the cubic meter and hectare measurements of DM from Drummond (1982). Although these RD 'hectares' are not a true measure of the area of mortality, they do retain the relationship of the relative importance of RD to DM indicated in the volume measurements.

Projected Risk—Projections of future importance of principal mortality agents are found in the Forest Service's Forest Health Protection national risk assessment project. The risk assessment project delineates general areas that are expected to experience 25 percent or more tree mortality over the next 15 years based on the expert opinion of professional pest management specialists. Although this risk assessment process is both coarse as well as iterative (changing as better numbers become available), current predictions provide us an opportunity to evaluate possible future changes in mortality agent importance. Information on future trends may help managers prepare for possible changes in coarse woody debris recruitment. Because of regional differences in data availability and mortality agent activity, modeling of expected mortality was left to the discretion of the regional Forest Service Forest Health Protection specialists. Risk assessment methodologies are discussed by Lewis (2002).

We used preliminary risk data (hectares) to create graphics showing the relative importance of the same five mortality agents used in the evaluation of the recent-past data.[3] Fire data for the risk assessment project was not obtained, but the insect and disease agents were comparable. Actual hectares will not be presented here, but eminent modifications in the risk data are not expected to greatly alter the relative importance of the various agents. However, in the more distant future, introduction of exotic insects and diseases, or dramatic changes in forest type or climate could cause significant shifts in realized agent importance.

Mortality Agent Groups: Patterns and Scale

Projected Risk—The projected risk data contains a more complete list of mortality agents than the five specific agents we used. In order to evaluate the importance of bark beetles as a group (including MPB) as well as defoliators (including WSBW) and other insects and disease, the risk data was partitioned into the following six agent groups: bark beetles (BB), defoliators (DF), other insects (IO), root disease (RD), dwarf mistletoe (DM), and other pathogens (PO). Organisms within each group include: mountain pine beetle, Douglas-fir beetle (*Dendroctonus pseudotsuga* Hopkins), spruce beetle (*D. rufipennis* [Kirby]), western pine beetle (*D. brevicomis* LeConte), Jeffery pine beetle (*D. jeffreyi* Hopkins), round-headed pine beetle (*D. adjunctus* Blandford), southern pine beetle (*D. frontalis* Zimmerman), pine engraver (*Ips pini* Say), fir engraver (*Scolytus ventralis* LeConte), and western balsam bark beetle (*Dryocetes confusus* Swaine) for BB; western spruce budworm and Douglas-fir tussock moth (*Orgyia pseudotsugata* [McDunnough]) for DF; balsam woolly adelgid (*Adelges piceae* [Ratzeburg]) for IO; annosus root disease, subalpine fir decline, and other unnamed root diseases for RD; various dwarf mistletoes (*Arceuthobium* spp.) for DM; and comandra blister rust (*Cronartium comandrae* Peck) and white pine blister rust (*C. ribicola* Fisch) under PO. The relative importance of each of theses groups was calculated and presented graphically for comparison.

Historical (1952)—The best data on historical mortality trends for most of the same six agent groupings was collected in 1952 (USDA FS 1958). The more recent forest health data (recent past) contained too much missing data to calculate adequate

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[3] Unpublished date on file (12/24/99), USDA Forest Service, Forest Health Protection (Washington and Regional Offices).

numbers for the BB, DF, IO, and PO categories. Because of the differences in the 1952 data standards, two graphics were created. The first graphic uses information from the year 1952 for mortality groups similar to those delineated for the risk data: bark beetle (BB), defoliators (DF), other insects (IO), root disease (RD), heart rot, and stem disease (includes DM, heart rot, and blister rust) (HR/SD), and other pathogens (PO). The second graphic uses trend data as determined in 1952 for the broader groupings of insects, disease, fire, and other (USDA Forest Service 1958, specifically, Basic Statistical Tables 17, 66, and 76).

Mortality of sawtimber (board feet) was chosen to be most comparable to our other data. Thus, information on growth loss and on growing stock was not used. As with all data in this study, hardwoods are minimal and were not separated from conifers.

The 1952 information was not available for the Forest Service Regions *(fig. 1)*. Instead, data was either given by state or by different regional areas. For example, in place of the Northern, Rocky Mountain, Southwestern and Intermountain Regions, the 1952 study combines these four Regions into two larger Regions: the Northern Rocky Mountains and the Southern Rocky Mountains. The Northern Rocky Mountains contains all of the Northern as well as part of the Rocky Mountain and Intermountain Regions (Idaho, Montana, South Dakota and Wyoming). The Southern Rocky Mountain contains all of the Southwestern as well as the remainder of the Rocky Mountain and Intermountain Regions (Arizona, New Mexico, Colorado, Utah, Nevada). Differences in the measure of impact (volume, not area) and in regional delineations complicate comparisons, but relative importance of mortality agents is expected to remain indicative.

Results

Patterns and Scale of Occurrence of Mortality Agents

The terms “impact” and “area affected” used in the following results and discussion should be clearly understood to avoid confusion in interpretation of the data. As noted previously, impact of a mortality agent on a tree can be measured as volume, number of trees, or area killed. Available data, however, limited us to the measurement of “hectares affected.” Thus, the word “impact” refers to this measurement of hectares only and should not be directly equated to “biological impact.” The term “area affected” should also be clarified. Although we are principally interested in dead trees, mortality data was not always available. For agents whose principal consequence is growth loss and not death, the relationship between the number of hectares affected and hectares that experienced mortality are unclear. Thus, for agents such as WSBW and DM many of the hectares affected may not have experienced mortality.

Specific Mortality Agents: Patterns and Scale

Historical (Recent past)—Examples of the differences in the scales and temporal patterns of the five specific mortality agents from 1978 to 1997 are presented for the Forest Service’s Northern Region *(fig. 2)* and the Southwestern Region *(fig. 3)*. As expected, area affected by insects (MPB and WSBW) and fire vary considerably from year to year, although long-term patterns often occur. MPB levels in the Northern Region show a clear example of an activity cycle spanning multiple years *(fig. 2).* RD and DM are more pervasive (more area affected) than insects and fire. The depiction of RD and DM effects using a straight-line average (annual values not available) does not display fluctuations known to occur in response to variations in environmental factors (e.g., drought stress). However, these yearly fluctuations are known to be less dramatic than those experienced by insects and fire (Dahms and Geils 1997, Drummond 1982, Smith 1984).

The average annual area affected (thousands of hectares/year) by MPB, WSBW, RD, DM, and for each of the six Forest Service Regions of the West was determined using regional data from 1978 through 1997 *(fig. 4).* Although numbers used for RD are not actually the 'area affected,' they do maintain the relationship between DM- and RD-affected volume. Interestingly, in the Northern, Rocky Mountain, and Southwestern Regions these calculations of RD hectares resemble the 'area of management concern' for RD presented in the 1985 forest health summary (DeNitto 1985). Also, comparison with other data for the Pacific Southwest shows that our relative area for RD preserves relationships among agents in terms of overall impact (USDA Forest Service 1979). The difficulty in interpreting these hectare totals lies in the disproportional area within each Region.

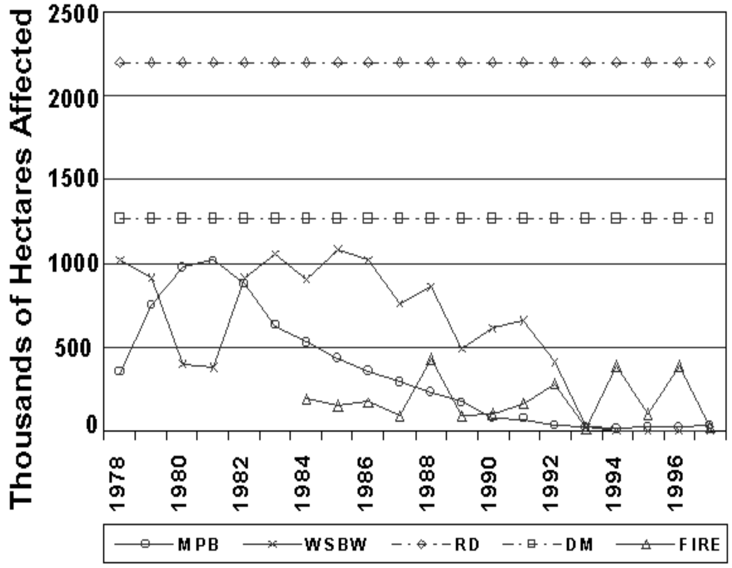

Figure 2—Fluctuation patterns of hectares affected by five specific mortality agents in the Forest Service's Northern Region, 1978-1997. Agents included mountain pine beetle (MPB) *(Dendroctonus poderosae),* western spruce budworm (WSBW) *(Choristoneura occidentalis),* root disease (RD) (most likely *Armillaria* spp., *Phellinus weirri*, *Heterobasidion annosum*, *Phaeolus schweinitzii*, and *Ceratocystis* spp.), dwarf mistletoe (DM) (*Arceuthobium* spp.), and wildfire (FIRE). Areas of WSBW and DM are affected hectares rather than hectares of mortality. In order to graphically display RD in terms of "number of hectares affected," a ratio was calculated using the available cubic meter measurement of RD mortality (Smith 1984) and the cubic meter and hectare measurements of DM volume loss (Drummond 1982). Although the RD "hectares" are not a true measure of area, they do retain the relationship of the relative importance of RD volumes to DM volumes. RD and DM are known to fluctuate somewhat, but these patterns have not been followed closely. FIRE numbers for the Northern Region are actually for Idaho and Montana rather than the Forest Service regional area.

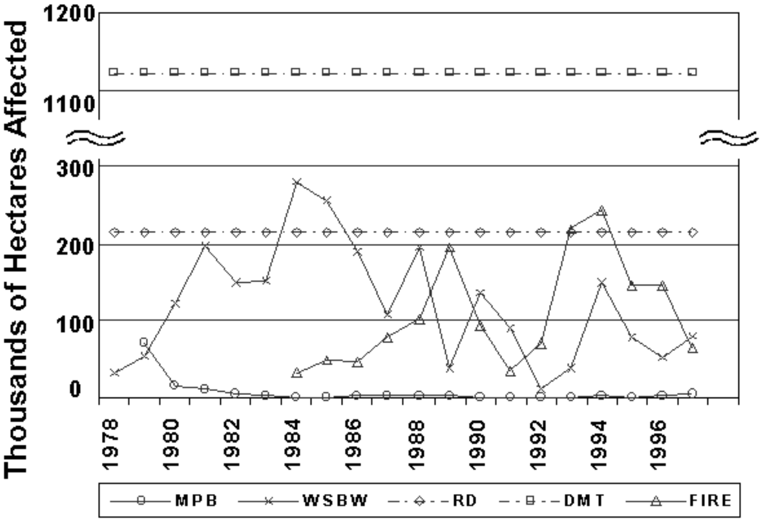

Figure 3—Fluctuation patterns of hectares affected by five specific mortality agents in the Forest Service's Southwestern Region, 1978-1997. Agents included mountain pine beetle (MPB) *(Dendroctonus ponderosae),* western spruce budworm (WSBW) *(Choristoneura occidentalis),* root disease (RD) (most likely *Armillaria* spp., *Phellinus weirri*, *Heterobasidion annosum, Phaeolus schweinitzii*, and *Ceratocystis* spp.), dwarf mistletoe (DM) (*Arceuthobium* spp.), and wildfire (FIRE). Areas of WSBW and DM are affected hectares rather than hectares of mortality. In order to graphically display RD in terms of "number of hectares affected," a ratio was calculated using the available cubic meter measurement of RD mortality (Smith 1984), and the cubic meter and hectare measurements of DM volume loss (Drummond 1982). Although the RD "hectares" are not a true measure of area, they do retain the relationship of the relative importance of RD volumes to DM volumes. RD and DM are known to fluctuate somewhat, but these patterns have not been followed closely.

All hectares affected by the five specific agents were combined, and the relative importance (as a percent of the total affected area) was determined for each Region *(fig. 5)*. This interpretation lacks the ability to show quantitative levels of agent impact (e.g., hectares/Region or hectares affected/hectares available). However, it does provide a basis for the evaluation of which agents may be principal in creation of coarse woody debris within a Region.

As expected, MPB is relatively important in the Northern, Rocky Mountain, Intermountain, and Pacific Northwest Regions where it attacks mostly lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) and some ponderosa pine (*P. ponderosae* Dougl. ex. Laws.) *(fig. 5)*. However, MPB is relatively less important in the Southwestern and Pacific Southwest Regions. WSBW incidence is widespread but is relatively more important in the Rocky Mountain Region. RD has been active in the Northern, Pacific Northwest, and Pacific Southwest Regions with some impact noted in the Southwestern and very little noted in the Rocky Mountain and Intermountain Regions. DM is the most active agent over the entire West and is particularly important in the Southwestern, Intermountain, and Pacific Southwest Regions. The limited number of hectares affected by other agents in these Regions would explain why DM shows higher importance in the southern Regions. Fire affects few hectares on average but is active in all Regions. Over the entire West, diseases affect a greater area than do insects and fire combined.

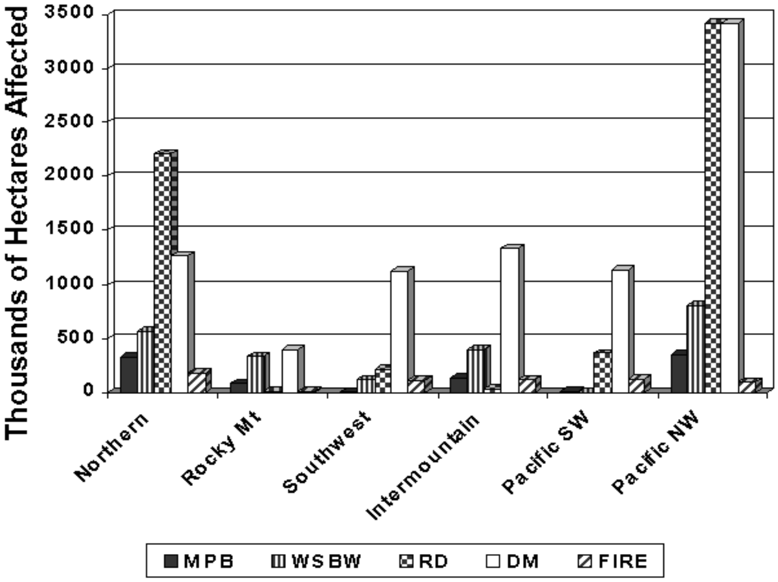

Figure 4—Average annual area (in thousands of hectares) affected by five specific mortality agents in each of six of the Forest Service's western Regions: recent past (1978-1997). Agents included mountain pine beetle (MPB) *(Dendroctonus ponderosae),* western spruce budworm (WSBW) *(Choristoneura occidentalis),* root disease (RD) (most likely *Armillaria* spp., *Phellinus weirri, Heterobasidion annosum*, *Phaeolus schweinitzii*, and *Ceratocystis* spp.), dwarf mistletoe (DM) (*Arceuthobium* spp.), and wildfire (FIRE). Areas of WSBW and DM are affected hectares rather than hectares of mortality. In order to graphically display RD in terms of "number of hectares affected," a ratio was calculated using the available cubic meter measurement of RD mortality (Smith 1984) and the cubic meter and hectare measurements of DM volume loss (Drummond 1982). Although the RD 'hectares' are not a true measure of area, they do retain the relationship of the relative importance of RD volumes to DM volumes. RD and DM are known to fluctuate somewhat, but these patterns have not been followed closely. FIRE numbers for the Regions are actually by state boundaries resulting in slightly different areas for the Northern, Rocky Mountain, and Intermountain Regions.

Projected Risk—The expected importance of the four insect and disease agents (fire excluded) over the next 15 years is based on predicted mortality (not growth loss) *(fig. 6),* which may explain the principal changes in importance between predicted and past agent importance. In the recent-past data MPB was not the principal active agent in any Region. However, when predicted mortality is considered, MPB is expected to be the principal mortality agent in half of the Regions (Rocky Mountain, Intermountain, and Pacific Northwest). RD was and is predicted to be the principal active agent in the Northern Region and is predicted to be the principal agent in the Pacific Southwest. In the Southwestern Region, DM is predicted to be the most important mortality agent, with considerable activity in the Pacific Southwest. Despite their large area of influence in all Regions during the past 20 years (recent past), predicted importance of WSBW and DM is much lower due to the minimal associated mortality.

Differences in agent past and predicted importance *(figs. 5, 6)* may be indicative of changes in host availability, advances in detection of agents, increased recognition of agent roles, differences between area affected (recent past) and area of mortality (projected risk), or differences in methodologies used to determine affected area. Small changes are also expected due to the exclusion of fire from the projected mortality data. We should note that relative importance of an agent over the entire western U.S. differs depending on whether relative importance (by hectares) or average percent importance (sum of percentages divided by six Regions) is used. These differences between relative importance values are due to the very high number of hectares of RD mortality predicted by the Northern Region.

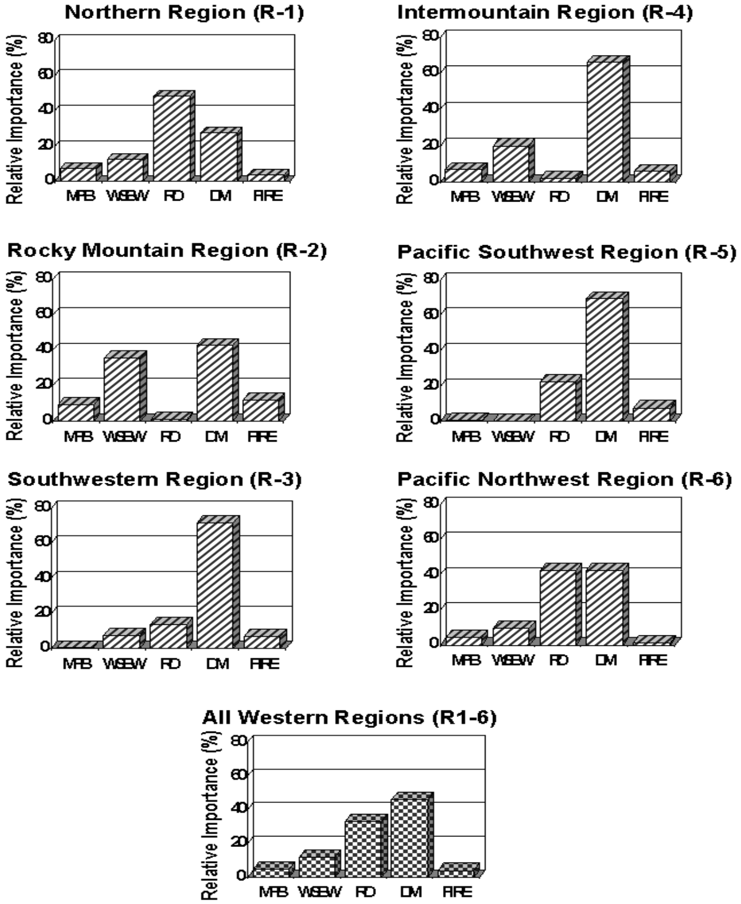

Figure 5—The historical relative importance of five specific mortality agents in the western U.S.: recent past (1978-1997). Agents included mountain pine beetle (MPB) *(Dendroctonus ponderosae),* western spruce budworm (WSBW) *(Choristoneura occidentalis),* root disease (RD) (most likely *Armillaria* spp., *Phellinus weirri*, *Heterobasidion annosum*, *Phaeolus schweinitzii*, and *Ceratocystis* spp.), dwarf mistletoe (DM) (*Arceuthobium* spp.), and wildfire (FIRE). Data from 1978 to 1997 were used to calculated annual averages. In some cases data was missing. MPB data was complete for 18 of the 20 years. FIRE data was available from 1984 to 1997 for a total of 14 years. Data for RD and DM were from the early 1980s. Importance of WSBW and DM are based on affected hectares rather than hectares of mortality. RD importance was calculated based on a ratio of the volume impacts of RD to DM. FIRE numbers for the Regions are actually by state boundaries resulting in slightly different areas for the Northern, Rocky Mountain, and Intermountain Regions.

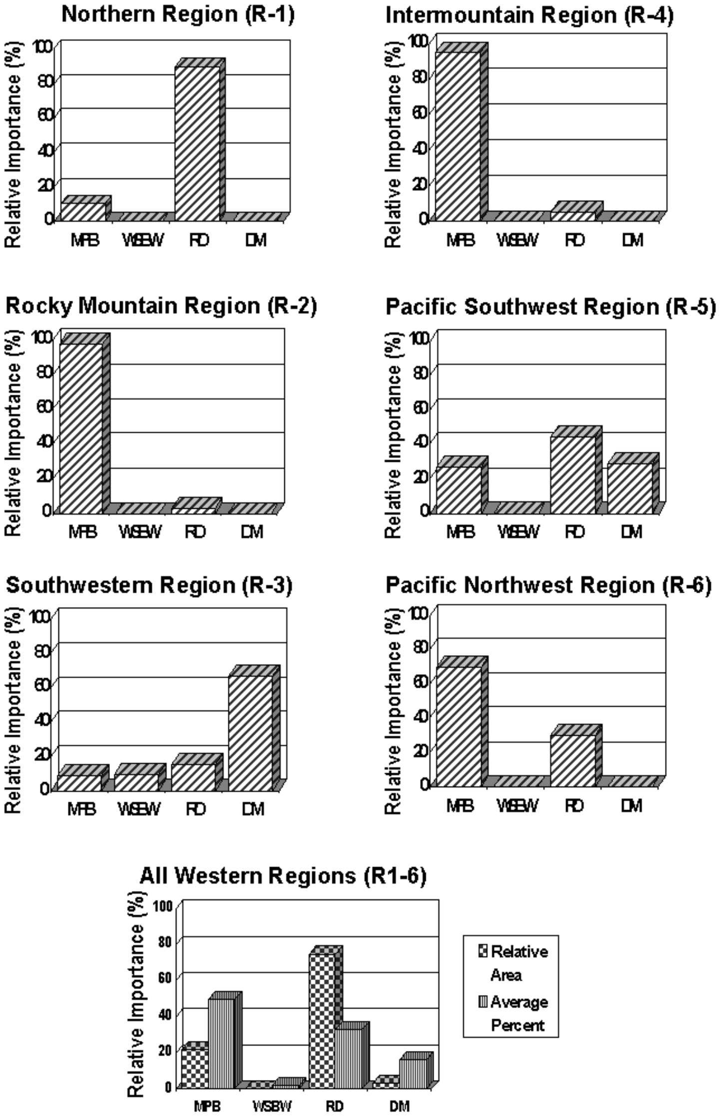

Figure 6—The predicted relative importance of four specific insect and disease mortality agents in the western U.S.: projected risk (2000-2015). Agents include mountain pine beetle (MPB) *(Dendroctonus ponderosae),* western spruce budworm (WSBW) *(Choristoneura occidentalis),* root disease (RD) (most likely *Armillaria* spp., *Phellinus weirri*, *Heterobasidion annosum*, *Phaeolus schweinitzii*, and *Ceratocystis* spp.), and dwarf mistletoe (DM) (*Arceuthobium* spp.). Data are from a Forest Service risk assessment project being conducted by the Washington, D.C. office and is preliminary only. Revisions are being completed by the Forest Service. However, relative importance relationships are expected to remain similar. Because FIRE is not graphed, the importance of each agent is not directly comparable to *figure 5.*

Mortality Agent Groups: Patterns and Scale

Projected Risk—Because of the inclusion of many other bark beetles species and of white pine blister rust (under other pathogens [PO]) *(fig. 7),* the expected relative importance of the "agent groups" differs somewhat from the "specific agents" *(figs. 5, 6).* MPB used in *figures 5-6* is only one of many important bark beetles of the western U.S. Risk data predicts MPB will contribute approximately half of the bark beetle mortality over the next 15 years in the Northern, Rocky Mountain, and Pacific Northwest Regions. In the Southwestern Region, MPB constitutes only about 7.5 percent of the predicted BB mortality, while in the Intermountain and Pacific Southwest, MPB constitutes only 13 and 22 percent, respectively. Additional mortality in the West is expected from Douglas-fir beetle, western pine beetle, round-headed pine beetle, Jeffery pine beetle, spruce beetle, fir engraver, western balsam bark beetle, and ips (*Ips* spp.).[3] Most Regions maintain similar importance profiles whether "specific agents" or "agent groups" are used. Only in the Southwestern and the Pacific Southwest Regions did MPB impact fail to represent BB impact. WSBW successfully represented DF in all of the Regions except Intermountain, where Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) is expected to cause considerable defoliation impact. Information indicates that insects other than BB and DF are not expected to contribute significant additional mortality to western conifers. However, recent and future exotic insect introductions could have considerable unpredicted impacts.

The "specific agents" and "agent groups" *(figs. 6, 7)* used the same hectare numbers for RD and DM quantities. Thus, changes in relative importance are due to changes in hectare values of the other agent groups. Notably, the inclusion of other pathogens (PO) was important in representing both historic and predicted impact of disease in the western U.S. In all Regions except the Pacific Southwest, the exotic white pine blister rust (included in PO) is predicted to cause significant areas of mortality.[3] In the Rocky Mountain Region, comandra blister rust is also expected to be important.[3] The relatively high RD impact is still evident in the Northern Region and influences the overall importance value of RD in the West when total hectares at risk are considered.

Historical (1952)—Data from 1952, using similar mortality agent groupings for slightly different regional delineations, shows a number of variations between historical and predicted importance values. In 1952 bark beetles were the primary source of mortality (by tree volume) over all Regions *(fig. 8).* Future predictions indicate the continued relative importance of bark beetles, except in the Northern Region where the dramatic increase in RD importance overshadows effects of all other agents. Both historical data and future predictions indicate limited DF mortality across the West with highest impact in the Southern Rocky Mountains. It is unclear which insect was responsible for the significant "other insect" mortality in California in 1952 *(fig. 8).* However, over the West, other insects (IO) besides bark beetles and defoliators have not had a large effect.

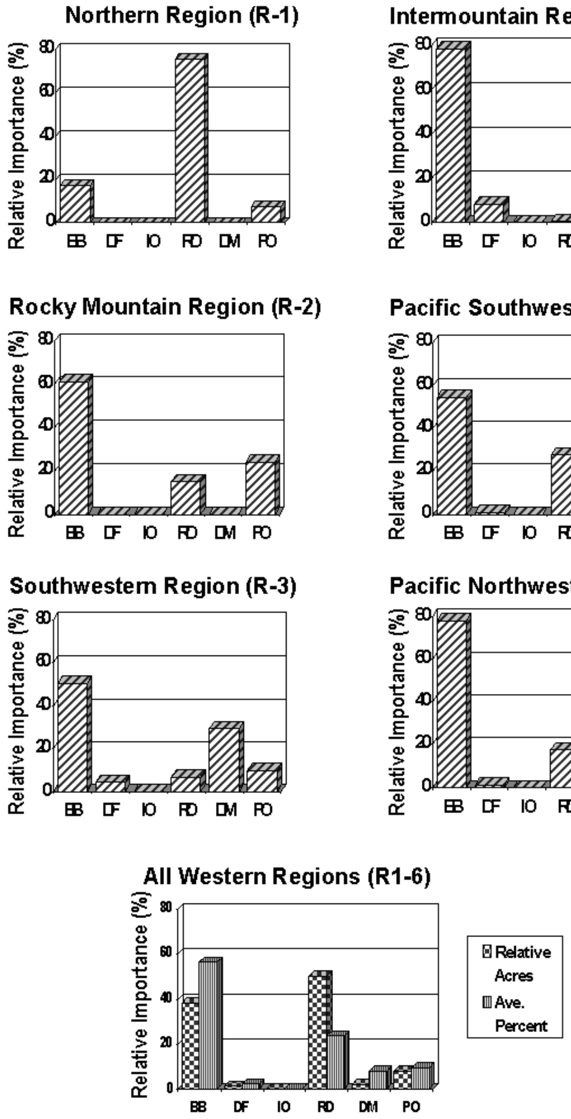

Figure 7—The predicted relative importance of six insect and disease agent groups in the western U.S.: projected risk (2000-2015). Agent groups are bark beetles (BB), defoliators (DF), other insects (IO), root disease (RD), dwarf mistletoe (DM), and other pathogens (PO). Organisms within each group include: Douglas-fir beetle *(Dendroctonus pseudotsuga),* fir engraver *(Scolytus ventralis),* pine engraver *(Ips pini),* Jeffery pine beetle *(D. jeffreyi),* MPB, roundheaded pine beetle *(D. adjunctus),* spruce beetle *(D. rufipennis),* southern pine beetle [in Arizona] *(D. frontalis),* western pine beetle *(D. brevicomis),* and western balsam bark beetle *(Dryocetes confusus)* for bark beetles; Douglas-fir tussock moth *(Orgyia pseudotsugata),* and western spruce budworm *(Choristoneura occidentalis)* for defoliators; balsam woolly adelgid *(Adelges piceae)* for other insects; annosus root disease *(Heterobasidion annosum),* subalpine fir decline, and other unnamed root diseases under root disease; various dwarf mistletoes (*Arceuthobium* spp.); comandra blister rust *(Cronartium comandrae)* and white pine blister rust *(C. ribicola)* for other diseases. Data are from a Forest Service risk assessment project being conducted by the Washington, D.C. office and is preliminary, only. Revisions are being completed by the Forest Service. However, relative importance relationships are expected to remain similar.

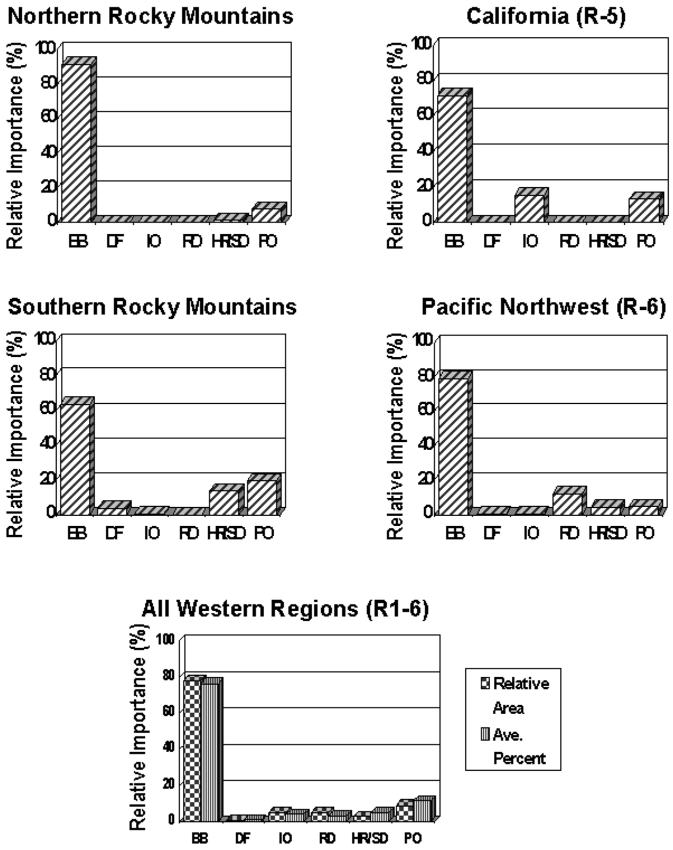

Figure 8—The historical relative importance of six insect and disease agent groups in the western U.S.: historical (1952). Regions in the 1952 data are different from the Forest Service Regions. In place of the Northern, Rocky Mountain, Southwestern and Intermountain Regions, the 1950s study combines these four Regions into two Regions; the Northern Rocky Mountains and the Southern Rocky Mountains. The Northern Rocky Mountains contains all of the Northern as well as part of the Rocky Mountain and Intermountain Regions (Idaho, Montana, South Dakota, and Wyoming). The Southern Rocky Mountain contains all of the Southwestern, as well as the remainder of the Rocky Mountain and Intermountain Regions (Arizona, New Mexico, Colorado, Utah, and Nevada). The six insect and disease agent groups include bark beetles (BB), defoliators (DF), other insects (IO), root disease (RD), heart rot and stem disease (HR/SD) and other pathogens (PO). Organisms within each group are not defined. However, IO includes borers, tipmoths, turpentine beetles, and balsam wooly aphid. RD is primarily Douglas-fir root rot (possibly *Phellinus weirii* = *Inonotus sulphurascens*). HR/SD is heart rot, blister rusts (*Cronartium* spp.) and dwarf mistletoe (*Arceuthobium* spp.). OP includes foliage and systemic diseases (*Elytroderma deformans* and pole blight). Differences in the measure of impact (volume not hectares) and in regional delineations complicate comparisons, but relative importance of mortality agents is expected to remain indicative. Data are from the year 1952 and are similar to trend data, except in the Northern Rocky Mountains where insect mortality was higher and disease mortality was lower than trends had indicated (USDA Forest Service 1958).

Historically, only the Pacific Northwest was noted for important RD mortality, while future expectations are of significant mortality in all Regions except the Intermountain (part of both the historic Southern Rocky Mountain and Northern Rocky Mountain Regions). In the 1952 data DM is grouped with heart rots and other stem diseases (HR/SD). This inclusion of other agents could explain why the historic Pacific Northwest HR/SD value *(fig. 8)* is higher than predicted DM values *(fig. 7)*. In the Pacific Southwest, however, the only explanation for the predicted increase in the DM value over the historic HR/SD is an actual increase in DM in the Region. Other pathogens have also changed. In 1952 elytroderma (*Elytroderma deformans* Darker) and pole blight were the principal "others," while future predictions denote white pine blister rust and comandra blister rust as important "other" pathogens. Primary causes for these differences likely include the use of volume impact (1952 data) in place of area, progress in understanding and detection of agents, differences in assigning causal agent in areas where many agents are active, and actual changes in forest susceptibility due to exotic pests, fire exclusion, and silvicultural practices (USDA Forest Service 1988).

Our analysis focused principally on insect and disease mortality agents, and on fire where data was available. It is important to remember, however, that there are other agents that can be locally very important in the recruitment of coarse woody debris. Mortality due to wind is very important in some regions, as are snow and ice, floods, drought, lightning, avalanches, animals, and suppression by other trees (USDA FS 1958, Harmon and others 1986, Parminter 1998). In the Rocky Mountain and Southwestern Regions, "other" agents may actually have caused greater mortality of sawtimber than insects, diseases, or fire (USDA FS 1958) *(fig. 9)*. In all Regions except the Pacific Southwest, "other" mortality was caused by weather with some animal damage. In the Pacific Southwest mortality was due to suppression by other trees. More recent regional information on mortality due to weather is patchy but indicates its continued importance (Harmon and others 1986). Also locally important may be the effects of pollution (e.g., air, water, or ground) (Carlson and Dewey 1971).

Discussion

Temporal and Spatial Scales of Coarse Woody Debris Recruitment

Recent mortality data (1978-1997) presented here show some of the differences in the spatial and temporal patterns of the various mortality agents *(figs. 2, 3)*. Such differences in disturbance regimes have been previously noted (Geils and others 1995, Parminter 1998) but not often quantified (see Swetnam and Betancourt [1998] for a quantitative example.) It is these differences in mortality patterns, as well as the character of the mortality agent, that affects the scales (spatial and temporal) of the coarse woody debris recruitment (Clark and others 1998, Li and Crawford 1994, Lundquist and others 1998).

This paper presents spatial scale only in terms of the number of hectares affected within a geo-political landscape unit (Regions) and does not give information on the distribution or extent of mortality incidences within the Region. For example, it is possible for an agent to create many small patches of mortality across the landscape, or to disturb a large contiguous area and yield similar values of hectares affected. However, literature on past effects of various disturbance agents does provide qualitative understanding of the possible differences in the spatial distribution of created dead wood. For example, epidemic MPB in monotypic stands of lodgepole pine are likely to create a larger, more continuous area of mortality than will Douglas-fir beetle in mixed forest type under endemic conditions.

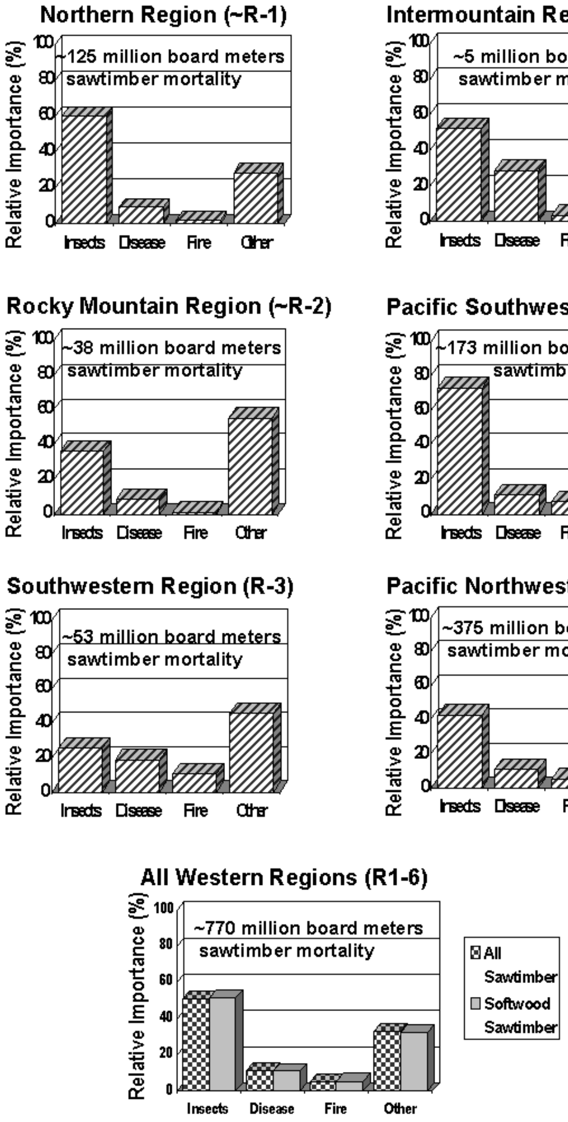

Figure 9—Relative importance of four mortality agent groups in the western U.S.: historical (pre-1952 trend). Region delineations differ from the Forest Service Regions. Because data were given by state, the Northern, Rocky Mountain, and Intermountain Regions had to be approximated using state boundaries (e.g., Northern Region as Montana and Idaho; Rocky Mountain as Wyoming, Colorado, and South Dakota; Intermountain as Nevada and Utah). The “other” category is principally suppression by other trees, timber harvest damage, weather, and animals. West and U.S. graphs show values for all sawtimber and softwood sawtimber on commercial lands (USDA Forest Service 1958).

Parminter (1998) makes two important points for understanding the differential spatial effects of agents. First, small-scale disturbances are the primary source of heterogeneity in forest structure and composition, including the dead wood component. Regular patches created by BB tree- or patch-attacks, RD pockets, or some windthrow events operate at the tree or stand level but cause landscape patterns and landscape consequences. Second, large-scale disturbances such as wildfire, blowdown, floods, and other often weather-related events act on all tree species, sizes, and ages, resulting in significant or complete mortality over a large area. Often the result is a shift in successional stage and sharp increases or pulses of coarse woody debris input. Additional discussion on the role of disturbance scale on the resulting ecosystem structure can be found in Holling (1992).

Data on the effects of agents over the past 20 years (1978-1997) *(figs. 2, 3)* exhibit annual differences, as well as possible long-term temporal patterns of mortality agents. For example, MPB activity shows a long-term cycle, while fire hectares appear to fluctuate greatly on a yearly basis. Likely, this is due to the population dynamics of the beetles and continuity of stand structure from year to year, as compared to the high variability of precipitation, temperature, wind, and humidity that greatly affect fire. Longer-term patterns in fire activity are not evident *(figs. 2, 3),* but have been found in long-term data sets (e.g., Swetnam and Betancourt [1998]). Seasonal variations, also, are not visible, but literature indicates that seasonal coarse woody debris recruitment often occurs in relation to seasonal weather patterns (e.g., heavy rains, wind, fire, floods, etc.). We should also note that, although hectares affected do not directly translate into mortality or amount of coarse woody debris created, *figures 2-3* do illustrate the dynamic variability inherent in the agents.

Differences in agent activity between Regions, such as the Northern and Southwestern, are indicative of the principal regional ecosystem processes at work *(figs. 2, 3).* For example, RD is much more active in the Northern than in the Southwestern Region while the opposite is true of DM. These differences are directly related to precipitation and principal forest types of the two areas. However, because these two Regions are not comprised of equal acreages, it would be incorrect to assume that DM has a nearly equal impact over the Northern as the Southwestern Region.

The Pacific Northwest has both the most forested hectares and the most commercial forest hectares of the six Regions (USDA FS 1958). Because of this larger area, agent impacts (as total hectares) are likely to appear greater in the Pacific Northwest than in smaller Regions *(fig. 4).* Data on the total number of hectares surveyed is not readily available, although reports indicate that more than just the commercial forested lands are surveyed. If hectares affected were related to average yearly hectares surveyed, some additional regional trends might be visible.

Although an agent may act principally at one spatial or temporal scale, it is important to recognize its effects at all scales (Parminter 1998). The determined importance of an agent on the ecosystem depends on which of these levels is being evaluated. For example, outbreaks of bark beetles such as Douglas-fir beetle can kill many trees at the patch or stand scale within 3 or 4 years. Yet, over the landscape, these clustered or widely dispersed groups of dead trees can create greater landscape heterogeneity over many decades (Parminter 1998). At the patch level the beetle may be described as a negative influence, killing trees. Yet, at the landscape level the positive effects of heterogeneity might be noted.

Differential Activity of Mortality Agents

In addition to differences in spatial and temporal scales of coarse woody debris recruitment, mortality agents produce types of dead wood that serve varying roles in the ecosystem (Bull and others 1997, Harmon and others 1986). A basic understanding of the differences in agent groups will augment further interpretation of the significance of the regional variations presented.

Bark beetles tend to be tree species- and size-specific, generally affecting trees already weakened, diseased, or otherwise stressed (Amman and McGregor 1985, Barbosa and Wagner 1989, Dahms and Geils 1997). The area affected may fluctuate annually with weather and stand conditions, but when considerable amounts of favorable host become suitable habitat, outbreaks can occur, killing trees over entire watersheds (Amman and others 1989). Defoliator populations are more influenced by favorable synchrony between host phenology and defoliator life cycles, and are often influenced by environmental factors, such as weather, stand and site conditions, and enemy populations (Barbosa and Wagner 1989, USDA Forest Service and others 1999, Wulf and Cates 1985). Although defoliators don't generally kill trees, they can have significant impacts with repeated and complete defoliation (Barbosa and Wagner 1989, Swetnam and Lynch 1989, 1993). The dead wood that remains after insect attacks is often in the form of snags (Harmon and others 1986). Longevity of these snags, rate of bark slough, amount of stem breakage, and other traits depends on factors such as the tree species, tree size, other biotic agents (e.g., heart rot, staining fungi, arthropods, other animals) and abiotic forces (e.g., soil type, wind, rain, fire, temperature) (Brown and others 1998, Dahm 1949, Harrington 1996, Lowell and others 1992, Morrison and Raphael 1993, Schmid and others 1985).

Diseases are numerous and their effects so variable that a generalization of effects is difficult. Disease species may act principally on one host species (e.g., DM) or have effects on several host species in an area (e.g., RD) (USDA Forest Service and others 1999). Regional variation in effects may be due to disease virulence, tree or species resistance, climate, and other site conditions (Hawksworth and Wiens 1996, USDA Forest Service and others 1999). In many ecosystems disease contributes little coarse woody debris directly but predisposes large areas to other killing agents such as bark beetles (Otrosina and Ferrell 1995). In other ecosystems, disease, especially RD, may directly contribute considerable amounts of coarse woody debris (Byler 1978). The types and sizes of debris created by disease are also variable (Lundquist and others 1998). RD may kill several tree species of various sizes, and often causes trees to fall, creating mostly downed material of many sizes. DM may cause only top-kill or dropping of infected branches (Hawksworth and Wiens 1996), while, in large western white pine (*Pinus monticola* Dougl. ex. D. Don), white pine blister rust can create large snags (Monnig and Byler 1992).

All fire size classes and sources of ignition were included in the fire data, yet these can be biologically very different. Actual effects of fire depend largely on the type of fire (e.g., ground, surface, or crown) and its intensity, as well as the tree species and stand structure. Low intensity fire (surface or ground) acts more like DF or DM in that it does not cause large-scale mortality. Such fire generally consumes the downed debris. Mortality that does occur is selective for less fire tolerant tree species and smaller individuals. High intensity crown fire, however, is different from most insects and disease in that it can kill all trees of all species, sizes, and ages over a large area. Mortality in high intensity fires is condensed in time and space, providing considerable dead wood in relation to the area affected. It is calculated that a single intense fire could create between 105 and 575 years' worth of "normal" coarse woody debris input (Harmon and others 1986).

The dead wood created by other, often weather related agents (wind, snow and ice, avalanches, and flood) will likely include many tree species and sizes as described for high-intensity fire. However, because the tree is killed "by force," the coarse woody debris is usually downed material with broken snags. Other forces such as lightning, animals, and suppression by other trees may be more tree-selective or act on smaller patches, resulting in more specific species or size class mortality visible as standing snags.

Wind has been noted as being a particularly important mortality agent in some regions. For example, hurricanes and typhoons have damaged large areas of coastal North America, Europe, and Asia (Harmon and others 1986). Smaller patches of wind damage are also possible and occurrence can range from chronic seasonal damage to sporadic high recruitment spikes. Damage may differ by forest type as well as by soil type, topographic position, and edaphic conditions (Harmon and others 1986). Wind can leave broken snags, but the majority of the coarse woody debris is downed material.

Implications of Findings for Ecosystem Managers

Kile and others (1991) noted that until the 1970s, the overall impact of RDs such as *Armillaria* had not been appreciated. Smith (1984) calculated that 18 percent of the tree mortality in the western U.S. was due to RD. Recent past and projected-risk data presented here indicate that RD may be an even more important factor in tree mortality and recruitment of coarse woody debris than recent literature has indicated. Areas where RD is a principal agent of mortality include the Northern and Pacific Northwest Regions *(fig. 5).* Projections also indicate that in the Pacific Southwest, RD is expected to be of increasing importance *(fig. 6).* A greater proportion of susceptible tree species (Douglas-fir [*Pseudotsuga menziesii* Franco] and true firs [*Abies* spp.]) in these areas could account for the greater impact compared to areas dominated by more resistant pines. Overall, it is expected that harvest practices (especially selective logging), fire exclusion, and mortality caused by white pine blister rust have resulted and will continue to result in less tolerant forests and increased incidence of RD (Castello and others 1995, Smith 1984).

All Regions throughout the West show high hectare impacts by DM during the past 20 years—the Southwestern, Intermountain, and Pacific Southwest Regions in particular *(figs. 4, 5).* The principal effect of DM is growth loss. However, increased DM would result in weakened trees that may succumb to secondary agents (e.g., BB) or environmental stress (e.g., drought) (Byler 1978, Wood 1983). Unfortunately, pulses of mortality due to these additional stressors have not been well documented but should be expected. The Southwestern and the Pacific Southwest Regions are predicted to experience DM as an important mortality agent in the years to come *(figs. 6, 7).*

Pathogens other than RD and DM have caused mortality in the past (pre-1952) and are projected to continue doing so in the future. Historically, pathogens of importance included elytroderma and pole blight. In the future, pathogens of importance in the Northern, Rocky Mountain, Southwestern, and Intermountain Regions are predicted to be white pine blister rust (exotic) and comandra blister rust.

The introduction of additional exotic pathogens could also cause significant future tree mortality.

BB have historically been the most important source of tree mortality in the western U.S. and, in 1952, made up 60 to 90 percent of insect- and disease-caused mortality *(fig. 8)*. With the exception of the Northern Region, mortality risk projections predict that 50 to 80 percent of insect- and disease-caused mortality in the next 15 years also will be due to bark beetles *(fig. 7)*. Except in the Southwestern and Pacific Southwest Regions, MPB is expected to be the principal BB. Differences in the resulting snags will depend on site conditions, tree species and pre- and post-mortality agents.

The principal DF in the West is WSBW, but Douglas-fir tussock moth is also noted (USDA Forest Service 1988). Although these insects can affect large areas, defoliation rarely results in death unless nearly complete defoliation occurs over 3 or more years, or secondary agents take advantage of the tree's stressed condition (van Sickle 1985). The only area that shows relatively high defoliation in the recent past is the Rocky Mountain Region *(fig. 5)*. High WSBW incidence is closely related to available host forests (Douglas-fir, true fir and spruce forest types), a history of fire exclusion and selective logging, and conducive climate patterns (Fellin 1985). Projected defoliation-related mortality (although limited) is expected in the Southwest (by WSBW) as well as the Intermountain, Pacific Southwest, and Pacific Northwest Regions (by Douglas-fir tussock moth) *(fig. 7)*.

Also of importance to dead wood recruitment is the build-up of dead wood during the period of fire exclusion, and the resulting increased incidence of catastrophic (high intensity) fire (Carlson and others 1995, Johnson 1995). In areas like the Southwestern Region where fire (low intensity) is the primary force cycling nutrients (Carlson and others 1995, Harvey 1994), the actual pathway through which the dead wood passes is altered by changes in fire regimes. Moreover, this history of fire exclusion has helped alter forest types across the West towards dense, multi-story stands of shade-tolerant, fire-intolerant tree species (Schmidt 1985). These new stands, in turn, have different insect, disease, and fire susceptibilities, and produce different types of coarse woody debris. Unique regional and forest-type fire regimes are well described in other literature (DeBano and others 1998, Mooney and others 1981, Swetnam and Betancourt 1990).

In general, management of insects and disease is management of the forest and use of proper silvicultural practices (Barbosa and Wagner 1989, USDA Forest Service 1988, USDA Forest Service and others 1999). For example, outbreaks of most bark beetles require a large amount of susceptible host of suitable size, age, and stem density (Amman and others 1977). Decreasing stem densities, removing the preferred hosts, and allowing controlled burning are all considered important strategies in control of most bark beetles (USDA Forest Service and others 1999). In many cases, these same practices may also be used to control other insects and diseases (Miller 1979). The idea is that insect and disease problems can be mitigated by increasing the vigor of the tree and decreasing the amount of susceptible host (Kegley and others 1997).

Implications for Ecosystem Processes

Changes in the regimes of deadwood recruitment can have effects on various ecosystem processes, including soil retention (physical), nutrient cycling (chemical), and wildlife habitat (biological) (Harmon and others 1986). For example, because orientation and size of coarse woody debris effects soil retention on slopes and in streams (Harmon and others 1986), large quantities of small 'jack straw' stems broken from an ice storm might not have the same soil stabilizing effect that large, ground-contacting root diseased trunks would have. Since logs from older trees decay faster than young trees (Harmon and others 1986), debris from MPB activity might exhibit faster nutrient cycling than that from a windstorm (due to beetles selecting the larger, older trees) (Amman and others 1977, Amman and McGregor 1985, Cole and Amman 1980). And in terms of wildlife habitat, a large tree with heart rot that succumbs to bark beetles differs from a small tree that falls from RD (Bull and others 1997) or a RD-created brush field (Monnig and Byler 1992).

Available information about changes in regional disturbance regimes may help determine regional changes in the coarse woody debris recruitment. For example, we would expect that historic low intensity, high frequency fires of the Southwestern Region would have created different coarse woody debris properties than the more recent high intensity, low frequency fires (Harvey 1994, DeBano and others 1998, Touchan and others 1994). And in the Pacific Northwest, the effects of white pine blister rust, selective logging, and fire suppression in changing forest type from pine to Douglas-fir and true firs have already begun to produce a higher incidence of RD (Kile and others 1991, Monnig and Byler 1992). In both examples, the resulting dead wood will influence insect communities, fire patterns, and numerous other biological processes.

Management of Coarse Woody Debris

Management of coarse woody debris must consider not only active mortality agents and needs for specific types of debris but also the interaction of the coarse woody debris within the ecosystem. The agents we have mentioned not only create woody debris but also may take advantage of dead wood created by other agents including humans. For example, bark beetles may build to epidemic proportions in blowdown or logging slash, and RD can proliferate via freshly dead root systems (stumps, snags, etc.; USDA Forest Service and others 1999). An understanding of the management of human created coarse woody debris and its interactions with insects and disease is important for forest managers. The influence of coarse woody debris on BB populations is just one of many considerations.

A good example of the importance of coarse woody debris management is the case of the pine engraver (*Ips pini* Say) in the Southwestern Region. Slash left from thinning or logging operations is often suitable habitat that allows for a dramatic population increase leading to pine engraver outbreaks. However, we know that proper treatment of the slash can prevent these population buildups. Preventative treatments emphasize cutting and disposing of trees in such a way as to dry out the slash, rendering it less suitable for beetle reproduction (Kegley and others 1997, Massey and Parker 1981, Wilkinson and Foltz 1982). In addition to outbreak prevention techniques, there are suppression techniques that can kill beetle larva, adult beetles, or disrupt future mating (Kegley and others 1997, Massey and Parker 1981, Shea 1994, Wilkinson and Foltz 1982).

If managers are interested in creating coarse woody debris for the ecological services it provides, it may be beneficial to look at both past and projected agent activity. Although we have presented mortality agents as isolated forces, interaction between agents is the rule not the exception (Rogers 1996). Geils and others (1995) note that most managers work at the gap or stand level. However, our analysis is at a much larger scale. A finer scale evaluation of the mortality agents and the forest types in the stands of interest will result in better management decisions.

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Comparing Deterioration and Ecosystem Function of Decay-resistant and Decay-susceptible Species of Dead Trees[1]

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Abstract

The pattern and rate of deterioration of dead trees vary by species, which leads to important differences in their ecosystem function. This is illustrated by two species with different modes of death and decay: yellow-cedar *(Chamaecyparis nootkatensis)* and western hemlock *(Tsuga heterophylla)*. The heartwood of yellow-cedar contains compounds that inhibit decay. Most yellow-cedar trees die standing and persist as snags with intact tops for 80 years or more. Western hemlock lacks these specialized heartwood compounds and exhibits a more rapid deterioration. Also, modes of tree death, heart rot levels, and type of saprophytic decay may differ considerably by stand age for western hemlock. A greater diversity of structures is produced by the death and deterioration of western hemlock than yellow-cedar.

Introduction

Our research on dead trees in southeast Alaska has two origins. For yellow-cedar *(Chamaecyparis nootkatensis),* we developed a snag class system and conducted ground surveys in an attempt to reconstruct the epidemiology (i.e., timing of onset and population changes) for the extensive mortality problem that this species is experiencing. A more applied continuation of that research led us to describe the patterns of deterioration and recovery of the dead yellow-cedar resource. A separate line of research has focused on the mortality of trees in the western hemlock *(Tsuga heterophylla)* dominated old-growth forests. Here, it was necessary to reconstruct mortality of canopy-level trees so that we could interpret the factors that were driving small-scale disturbance in these forests. An applied aspect of this latter research is to evaluate the extent to which the factors that contribute to structural diversity and small-scale disturbance are maintained after different silvicultural treatments.

The objective of this paper is to contrast what we have learned about the death, decay, and ecosystem function of these two tree species: yellow-cedar and western hemlock.

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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Snag and Log Classification Systems

Existing snag and log classification systems proved to be inadequate for our use in both tree species. Such schemes (Cline and others 1980, Maser and others 1979) typically have classes in which tops progressively break, gradually reducing the heights of snags through time. For yellow-cedar, our early observations indicated that dead trees do not appear to have their tops break repeatedly as they deteriorate. For western hemlock, a tree species that contains considerable heart rot as a live tree in old forests, classifying snags and logs based on the decay levels of wood was not appropriate. Otherwise, some live trees or recently-killed trees would by classified as dead long ago. One of our objectives is to reconstruct tree mortality patterns through time (i.e., establish epidemiology rather than simply report structural condition of dead trees). Thus, we needed to use characteristics other than wood decay to distinguish groups of dead trees. We chose to develop a new system where we focused on the presence of primary limbs, secondary limbs, and twigs; we suspected that their presence was a more reliable indicator of how long trees had been dead. For western hemlock, our classes were aligned with an established snag and log decomposition system (Maser and others 1979, *table 1).*

Table 1—*Description of the snag/log class system and time-since-death estimates for each class of dead overstory trees of yellow-cedar (Hennon and others 1990) and western hemlock.*[1]

	Yellow-cedar		Western hemlock	
Structures retained, soil contact	**Snag/log class #**	**Mean, time-since-death (yrs)**	**Snag/log[2] class #**	**Range, time-since-death (yrs)**
Foliage	1	4	-	-
Twigs	2	14	1	0-12
Secondary branches	3	26	2	12-33
Primary branches	4	54	3	33-63
No limbs	5	81	4	63-117
Bole broken at soil level	6	Not dated	-	-
Integrated into soil	-	-	5	Not dated

[1] Unpublished data on file at the Department of Natural Resources, Division of Forestry, Ketchikan, AK.

[2] For western hemlock, our snag/log classes 1 through 4 align with snag stages 3 through 6, respectively, as described by Maser and others 1979; for downed material, our snag/log classes align with their log decomposition classes as follows, respectively: 1=1; 2 and 3=2; 4=3; 5=4 and 5.

We used two methods to date the death of yellow-cedar snags (Hennon and others 1990b): determining radial growth release of previously suppressed western hemlock and mountain hemlock *(Tsuga mertensiana)* that grew directly beneath larger yellow-cedar snags, and counting annual growth rings from a strip of callus tissue that connected one or more live roots to a single live branch in yellow-cedar trees that had a dead top and most of the bole was dead. For dead western hemlock, we determined time-since-death by finding trees cut and left at known times of partial timber harvesting (n=16), counting annual rings in wounds of adjacent trees that were scarred when live trees were windthrown (n=20), and aging conifer regeneration that had established on downed logs (n=15).

The snag/log classification systems that we develop for yellow-cedar and for western hemlock and average time-since-death for each class are given in *table 1*.

Note the comparable time-since-death for dead cedar and hemlock with similar branch conditions. The condition of the wood and persistence of snags standing for the two species are extremely different, however.

Patterns of Deterioration

The difference in heartwood chemistry between yellow-cedar and western hemlock is the key to understanding the vastly different pattern and rate of wood deterioration. Yellow-cedar has generally received little research attention until recently, but its heartwood chemistry is quite well known. Of the compounds reported in yellow-cedar heartwood *(table 2),* only nootkatin and chamic acid have been tested for their biological activity against fungi. Nootkatin is active at concentrations as low as 0.001 percent (Rennerfelt and Nacht 1955). These various compounds give the heartwood its color and aroma, as well as the wood's classification as being "resistant or very resistant" to decay (Forest Products Laboratory 1987). Western hemlock heartwood lacks these specialized compounds and is known as "slightly or non-resistant" to decay (Forest Products Laboratory 1987).

Table 2—*The known heartwood constituents of yellow-cedar (Hennon and Harris 1997).*

Compound	Identification, conformation, synthesis, or assay
Alaskene	Marx and Lewis 1973
Carvacrol	Erdtman 1952, Carlsson and others 1952
Chamic acid[1]	Carlsson and others 1952, Erdtman 1955, Rennerfelt and Nacht 1955, Erdtman and others 1956, Nordin 1964, Gensler and Solomon 1973, Nordin and others 1982
Chaminic acid	Erdtman 1955, Erdtman and others 1956, Nordin 1964
Chanootin	Nordin 1964, Karlsson and others 1973
Isochamic acid	Nordin 1964
Nootkatene	Erdtman and Topliss 1957
Nootkatin[2]	Aulin-Erdman 1950, Campbell and others 1952, Erdtman and Harvey 1952, Carlsson and others 1952, Duff and Erdtman 1954, Duff and others 1954, Johnson and Cserjesi 1975
Nootkatone	Erdman and others 1962, Ishida and others 1970, Odom and Pinder 1972, Dastur 1974, Yanami and others 1980
Valerianol	Odom and Pinder 1972
Vetivone	Dastur 1974

[1] Active against fungi at 0.01 percent (Rennerfelt and Nacht 1955).
[2] Active against fungi 0.001 percent (Rennerfelt and Nacht 1955).

For trees that die standing, yellow-cedar and western hemlock show differences soon after death. The needles on dead western hemlock trees are shed within a few months after trees die, but the scale-like foliage of yellow-cedar trees adheres to twigs for several years *(table 1).* Bark becomes loose and begins to slough away within several years for both species. The sapwood of both cedar and hemlock is colonized by fungi that initiate stain and wood decay. These sapwood fungi and other wood decay fungi continue their decay in the heartwood of western hemlock. Until this stage, the deterioration of the wood for the two tree species does not differ appreciably, but profound differences appear later. Eighty years after death, the penetration of decay in yellow-cedar wood is typically limited to less than 4 cm *(fig. 1).* Finally, approximately a century after death, soil-borne fungi create sufficient decay in the wood at the ground level so that the limbless tree boles of yellow-cedar break and fall. Soil-borne fungi are less influenced by yellow-cedar's heartwood compounds than other fungi (DeGroot and others 2000).

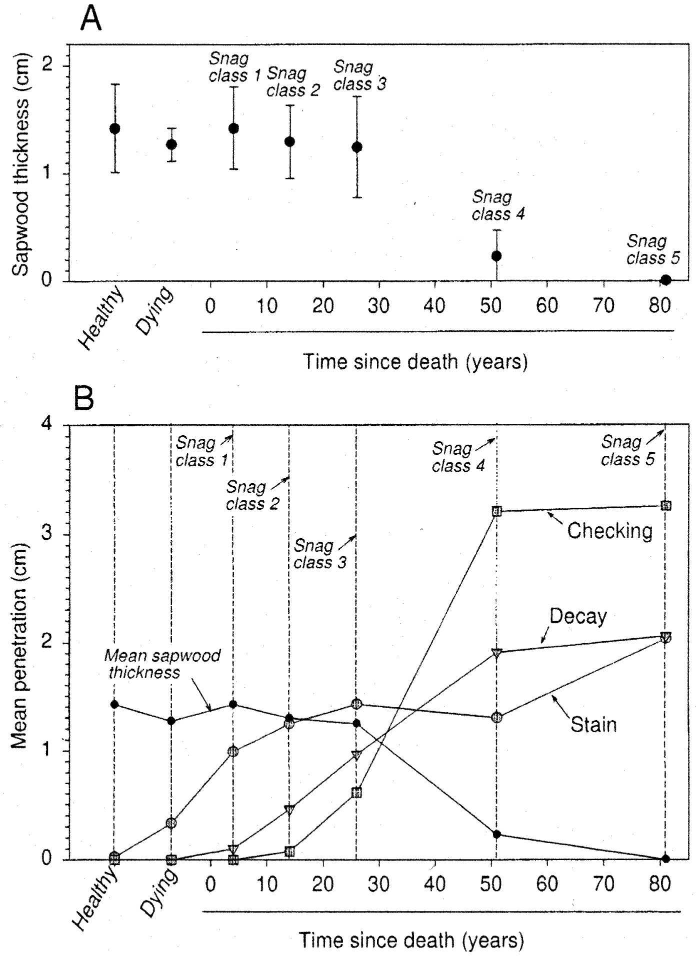

Figure 1—(A) Sapwood width, and (B) radial penetration of stain, decay, and checks (cracks) into the wood of yellow-cedar trees by classes of live trees, dying trees, and five snags.

For western hemlock, the decay process continues relatively unchecked as fungi penetrate into the heartwood. One fungus, *Fomitopsis pinicola*, causes a great amount of the decay in both the sapwood and heartwood. It degrades wood chemically in a process that selectively removes cellulose (i.e., brown rot) and leaves a residue of partially-modified lignin. A white rot fungus, *Ganoderma applanatum*, is also common as a wood decomposer of dead hemlock. As decay develops in the bole of dead hemlocks, the tops break, reducing the heights of snags in a pattern similar to many other conifers. We observed dead hemlocks 38 years after they were killed standing on Cat Island in southeast Alaska (Hennon and Loopstra 1991). Only one of

42 hemlocks had a standing portion taller than 10 m and most had broken within a few meters of the ground. The wood from all of these dead hemlocks was in a condition of advanced decay, most commonly colonized by *F. pinicola* or *G. applanatum* or both. These logs were all in the class 3 to 4 conditions *(table 1)*. In the final stages of decomposition, tree boles of western hemlock become fully incorporated into the soil (Graham and Cromack 1982).

Which Trees Die? How Do They Die?

Most dead yellow-cedar trees within the stands experiencing yellow-cedar decline are overstory trees that died standing (Hennon and Shaw 1997). Of the more than 250 dying yellow-cedars that we have monitored for nearly 20 years, fewer than 2 percent have died by uprooting or bole breakage. Declining yellow-cedar forests cover more than 200,000 ha in Southeast Alaska. In declining stands, dead yellow-cedars in all five standing snag classes made up two-thirds of the yellow-cedar basal area (Hennon and others 1990a).

The type of tree death for western hemlock is more variable and is influenced by stand age. Hemlocks dying in young-growth forests are predominantly small, suppressed trees that die standing from competitive stresses. Biotic agents are not generally important tree mortality factors in these stands. Uprooting of young trees is usually caused by the collapse of unstable organic rooting substrates (such as decaying logs or stumps) and not by wind.

Recently, we sampled tree mortality in a maturing even-aged stand near Sitka, the oldest known clearcut in Southeast Alaska. Many western hemlock trees had died standing, but many also died through bole breakage *(table 3)*. Unlike in younger stands, much of the mortality in this stand was of the largest dominant trees. We suspect that much of this damage was from wind or snow loading and that these trees were predisposed to break because of their excessive height: diameter ratio. Heart rot was not involved with tree death in this stand.

In old-growth forests, western hemlock trees die standing, by bole breakage, and by uprooting. Many agents kill standing hemlocks; heart rot and gravity or wind often lead to bole breakage; and storms with associated heavy precipitation and wind cause much of the uprooting in upland forests. When large trees die by any of these mechanisms, gaps appear in the canopy and contribute to small-scale disturbance. We sampled 1180 dead hemlock trees in 27 old-growth stands in Southeast Alaska (Hennon and McClellan 1999) and found that uprooting is not the principal form of tree mortality, unlike in Washington (Graham and Cromack 1982). In reconstructing tree mortality, death by uprooting can be interpreted long after tree death because of the presence of the upturned root system. Distinguishing death as a standing tree or by bole breakage is more challenging because dead standing trees deteriorate and are reduced in height until they acquire the same broken-off, stump-like structure as that of trees that die by bole breakage. Our reconstruction showed that western hemlock trees most frequently die standing, fewer died from bole breakage, and fewer yet died from uprooting *(table 3)*.

Table 3—*Origins and functional characteristics of woody debris produced by three forms of tree mortality of western hemlock in different stages of stand development of upland forests in southeast Alaska. Type of tree mortality is very common (++), common (+), or uncommon (-) for each forest stage.*

Stage of stand development	Dead standing	Bole breakage	Uprooting	Predisposing factors	Relative size of affected trees	Decay condition upon falling[1]	Primarily brown or white rot[2]	Hollow logs[3]	Root system attached[4]	Soil mixing[5]
Early young-growth (< 100 yrs)	++			Competition-suppression	smallest	decayed	brown, white?	no	no	no
		-								
			+	Unstable rooting substrate	smallest	undecayed	brown, white?	no	yes	no
Maturing young-growth (100 to 250 yrs)	++			Competition, other	all sizes	decayed	brown	no	no	no
		++		Small diameter/height ratio	tallest	undecayed	brown	no	no	no
			-							
Old-growth (>250 yrs)	++			Competition, diseases, insects	all sizes	decayed	brown, white	some	no	no
		+		Heart rot, gravity, wind, snow/ice	large	decayed	white, brown	frequent	no	no
			+	Wind, saturated soils, snow/ice	all sizes	undecayed	brown, white	some	yes	yes

[1] Standing trees become partially decayed before falling to the forest floor and into streams; bole breakage in old-growth often produces logs that are pre-decayed by either white or brown rot before falling; trees that uproot likely have less extensive heartrot while live

[2] Most deterioraton of dead western hemlock is by the brown rot process, but, in Washington, Edmonds (1998) reports more white rot than brown rot in dead young-growth conifers. White rot may occur in old trees before any form of tree death.

[3] Hollow logs are produced by white rot fungi in live trees, are common in hemlocks with all 3 types of mortality, but most common in trees that die die by bole breakage

[4] Attached root systems can function as an anchor for less mobility of woody debris in streams and rivers; birds may nest in upturned root systems

[5] Soil mixing of organic and inorganic layers produced by uprooting may improve site productivity for tree growth

Ecosystem Roles of Dead Yellow-cedar and Western Hemlock

For yellow-cedar, three insects (a bark beetle *[Phloeosinus cupressi],* one or more longhorned beetles [e.g., *Opsimus quadrilineatus*], and a woodwasp [*Sirex* sp.]) are common in dying trees and class 1 snags but have completed their life cycles and abandoned the snags just 2 years after tree death (Schultz, pers. comm.) *(fig. 2).* The larvae residing under bark and the emerging adults are both potential food items for foraging birds. Little insect activity appears to occur in dead standing trees after they reach the class 2 stage. Loose and hanging bark could provide habitat for roosting bats on snags dead up to 14 years. We are beginning to evaluate these possible wildlife uses of each of the snag classes, but little is currently known about the extent to which dead cedars are used. Cavity nesting is apparently rare in dead yellow-cedars, likely because of the undecayed condition of heartwood even 81 years after death *(fig. 1).*

Johnson (1997) found a high rate of landslides associated with dead yellow-cedar forests on steep slopes where most of the trees were in snag class 4 (dead approximately 54 years). This probably occurs because the roots of these snags are decayed to the extent that hillsides become unstable (Johnson and Wilcock 1998). We know little about the deterioration of dead yellow-cedar trees and their interaction with soil processes and vegetation once they reach class 6, roughly 100 years after death. Possible roles of these downed yellow-cedar logs as they decay could be hiding cover for small mammals, seedling establishment for trees and other vegetation (i.e., nurse logs), and a nutrient source and substrate for roots, mycorrhizae, and soil invertebrates. Where yellow-cedar grows and dies in riparian areas, woody debris produced by this tree would likely persist as long or longer than any other wood in southeast Alaska. Thus, ecosystem function for dead yellow-cedar appears to be greatest immediately after tree death, is limited for above-ground processes as snags remain standing, and may increase about 100 years after tree death when snags break and fall to the forest floor.

Understanding the type of tree death for western hemlock is important because of the dominance of this species in the forests of coastal Alaska and the wide range of structures and processes that result from the different forms of tree mortality *(table 3).* Some structures are uncommon or absent during particular stages of forest stand development; also, several structures can only be produced by a specific form of tree death.

For example, uprooting of large conifers is the only form of tree mortality that produces large, dead trees with an attached root system. Uprooting mixes the inorganic and organic soil layers, counteracts some effects of soil development, and may maintain site productivity (Bormann and others 1995). In contrast, there is no soil mixing with trees that die standing or by bole breakage. When small trees in young-growth forests sometimes uproot on unstable, decayed woody substrates, they do not affect inorganic soil layers. The large anchoring root system attached to dead conifers that uproot in old-growth riparian forests may limit their mobility as woody debris and thereby enhance their function in streams and rivers.

Hollow logs develop with the combination of white rot fungi and tree response (i.e., "compartmentalization") in live trees. Heart rot of western hemlock is extremely common in old-growth forests of southeast Alaska where 30 to 40 percent of the volume of live trees is defective and 62 percent of this decay is white rot (Kimmey 1956). Heart rot levels are directly proportional to tree and stand age in southeast Alaska (Farr and others 1976) with little to none occurring in forests younger than 100 years (Kimmey 1956).

Dead standing trees and downed logs, whether colonized by heart rot fungi before death or decayed after death, can function as important habitat for a wide range of wildlife species, both large and small (Maser and others 1979, 1988). At least twelve species of birds rely on tree cavities for roosting and nesting in southeast Alaska (Hughs 1985). But snags of western hemlock have a limited persistence as a dead standing tree. Our observations on 42 western hemlocks made 38 years after they were intentionally killed indicate two outcomes: 37 percent broke at the lower bole before developing extensive decay and then they decomposed intact on the ground, and 63 percent developed decay as a standing dead tree and then shattered into many fragments upon impact with the ground (Hennon and Loopstra 1991).

Most hemlock mortality in young forests involves small trees that die standing from suppression. Fungi colonize these small dead stems and their wood is partially decomposed before falling to the forest floor or into streams. Thus, woody debris produced in these young forests may provide a limited function compared with old-growth forests because of small piece size and lack of an attached root system. The decomposition process of conifer wood may differ between young and old forests as well; Edmonds (1999) reports that wood decay of conifers in young-growth forests may favor white rot fungi over the more common brown rot found in old-growth forests. Repeated short rotations of young-growth forest could reduce the effects of brown rot, which produces stable residues that can contribute 30 percent of the volume in the upper layers of soil (McFee and Stone 1966). Generally, the variable type of tree mortality and the responding number of structures and processes in old-growth forests probably contributes to the structural diversity present in old-growth forests of southeast Alaska (Alaback 1982).

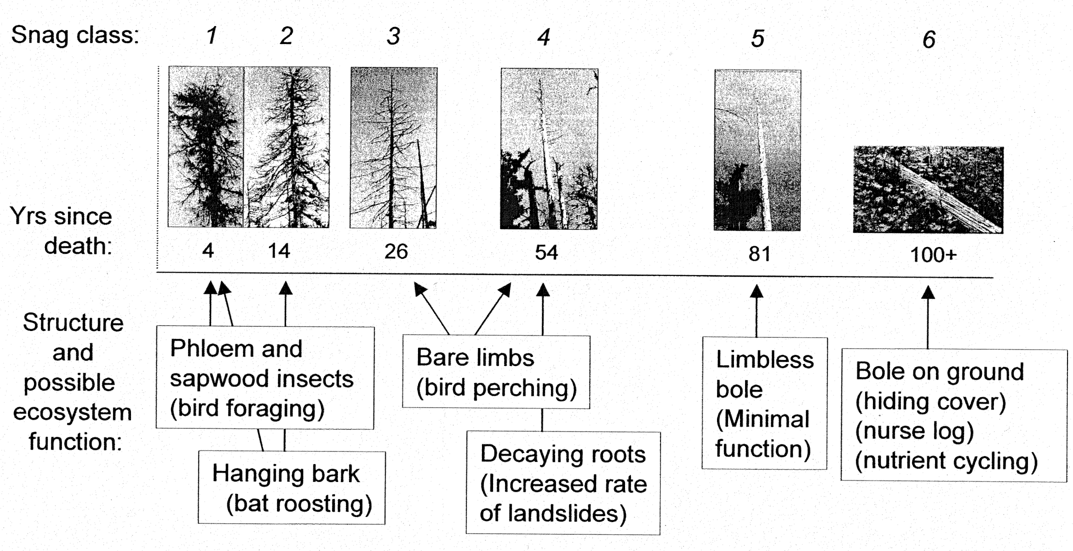

Figure 2—Potential ecosystem function of dead trees in each of the snag classes for yellow-cedar in southeast Alaska.

Summary

The defensive compounds in the heartwood of yellow-cedar alter the rate and pattern of deterioration in dead trees. Perhaps one compound, nootkatin, is responsible for the differences in decay between dead yellow-cedar and western hemlock trees and the corresponding structures that are produced. The tree containing this compound in its heartwood stands after death for nearly a century, possibly producing little in the way of terrestrial wildlife habitat, and finally breaks at the ground level to be decayed by soil organisms. The tree whose heartwood lacks this compound deteriorates rapidly, standing for a few decades at most, is used by many organisms in the complex number of structures produced, and falls to the forest floor where it becomes an integral part of the humus layer of soils.

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Influence of Fire on the Dynamics of Dead Woody Material in Forests of California and Southwestern Oregon[1]

Carl N. Skinner[2]

Abstract

The frequent occurrence of fire in most forested areas of California and southwestern Oregon before this century has been well established. Likewise, the importance of dead woody material to various wildlife species as snags and downed logs has been well documented. It is unlikely that much large woody material survived fire long enough to decompose fully in fire regimes that preceded the fire-suppression era. Observations of fire effects on dead woody material, as well as some recent limited data, indicate that fire often consumes most material that is in advanced stages of decay. However, though many appear to be consumed as well, hard snags and logs may, at least in part, survive low severity fires. Fires also help to create snags and, ultimately, downed logs. The frequent low-moderate-severity fires that characterized much of the forested landscapes of California and southwest Oregon burned with varying severity related to topography and weather conditions. The probable result was a landscape with many of the snags and logs clustered both in time and in space and very sparsely distributed in the intervening time and space.

Introduction

Although dead woody material (DWM; snags and logs) is recognized as having great importance for many wildlife species and ecological process (Harmon and others 1986, Hunter 1990), little information is available concerning its interaction with fire before the implementation of fire suppression. As a result, a great deal of uncertainty exists about the long-term role of fire in the dynamics of DWM. Most information that exists about DWM has been developed in temperate forests outside of areas classified as Mediterranean or in forests that have experienced artificially long periods without fire (Harmon and others 1986, Harmon and others 1987, Hunter 1990). Such studies provide little information concerning the historical interactions of fire and dynamics of DWM in forests that developed under the influence of chronic, frequent, low-moderate-intensity fires. Indeed, when the effects of fire are discussed, it is usually in terms of stand destroying events that create large amounts of DWM that then becomes available to the system (Spies 1997). Fire is not usually treated as a recurring ecological process that may have often removed more dead wood than it added. However, the latter was probably characteristic of the type of fires that were common in the forests of southwest Oregon and California (Agee 1993, Skinner and

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Chang 1996, Taylor and Skinner 1998). Persistent, recurring fires in concert with other agents of change (e.g., wind, insects, disease) created the conditions and habitat that wildlife in these areas adapted to and lived with before fire suppression and other management activities of the 20th century. Fire ecologists recognize that conditions in today's forests are probably, at least in part, an artifact of many decades of fire suppression (Agee 1997, Chang 1996, Taylor and Skinner 1998).

Fire: An Ecological Process

Fire history studies provide strong evidence that fires of the past occurred quite frequently—many times within the life spans of the dominant tree species (Skinner and Chang 1996). Unlike today, fires of the past did not occur as unusual isolated events. Rather, they occurred regularly and greatly influenced the development of forest conditions (habitat) (Agee 1993, Chang 1996, Skinner and Chang 1996, Mohr and others 2000). Thus, it is more appropriate that fire be viewed as a persistent ecological process rather than as a single event. The forest conditions (habitat) historically available to wildlife were those created and maintained by this process. Indeed, the late-successional forests of today have a long history of frequently recurring fire during their development (Taylor and Skinner 1998).

However, over the 20th century, fire suppression has been successful in limiting the cumulative area burned by fires. The result is that fire has become the exception rather than the rule (Husari and McKelvey 1996). Although we may have some sense of effects associated with individual fires of abnormal severity, we have only limited understanding of the effects of incessant, recurring fires of mostly low-moderate intensity with which these forests originally developed (Agee 1997). It is likely that the interaction of fire and dead wood dynamics were very different under historical fire regimes than those of today. A fire regime in which fires burn only infrequently and often severely will probably produce very different long-term habitat trends than a fire regime in which fire is a frequent visitor and is characterized by mostly low and moderate severity. The former serves mostly to add dead wood to the system in pulses and may lead to a boom-and-bust cycle of DWM. The latter is more likely to limit the accumulation of dead wood over both space and time (Kauffman 1990) and may result in less extreme variations of DWM.

It is necessary to consider both the ecological role and physical potential of fire in these forests in order to increase the long-term likelihood for success of management strategies (Millar and others 1998, Skinner and Chang 1996). Natural resource managers are attempting to balance what is thought to be best in terms of accumulations of DWM with the reality of an environment that tends to burn frequently. It is well known that, although fire spread is mostly related to smaller-sized (fine) fuels, the severity of fire effects and difficulty of fire suppression are primarily associated with the total amount of fuel available and consumed (Martin and Brackebush 1974). As DWM accumulates under a fire suppression management regime, fire hazard increases, often dramatically (Kauffman 1990). In order to assess realistically the likelihood of long-term success of various management strategies, it is necessary to understand why fire was historically frequent in the forests of southwestern Oregon and California and then to consider the ecological role of fire.

Climate

A fundamental reason that fire is an integral factor in the dynamics of forests of California and southwest Oregon is climate. This region has a Mediterranean climate characterized by hot, dry summers and cool, wet winters. Although this climate provides ample annual precipitation to grow productive forests, there is a pronounced annual drought. The Mediterranean climate guarantees that, even in years that are much wetter than average, the conditions for fire to spread easily are achieved annually in the dry season (Stine 1996). Considering the features of the Mediterranean climate and the fact that fire history research shows that fires were generally frequent, it is logical to surmise that fires regularly influenced the patterns and accumulations of DWM.

Dynamics of Dead Woody Material in Forests of Mediterranean Climates

Because of spatial and temporal patterns of fire frequency, severity, and seasonality, fires are likely to have influenced the spatial and temporal patterns of DWM accumulations in historical landscapes. Variation in fire regime parameters probably contributed significantly to and helped support habitat and species diversity (Martin and Sapsis 1992). The variation within the fire regime at broad, landscape scales helped contribute to the dynamics of habitat pattern over time (Agee 1998). However, few landscape-scale, fire-history studies have been undertaken, primarily because of time and costs involved (Skinner 1997a). Most fire history studies have been conducted on small areas or a few plots that were widely scattered over large areas. Fire ecologists are just beginning to understand fire regimes at landscape scales. The interpretation of the dynamics of fire and vegetational patterns at the landscape scale are primarily focused on live vegetation because little DWM survives from before the fire suppression era except in rare cases. Even so, recent landscape-scale, fire-history studies may eventually help in understanding historical patterns of DWM through describing the developmental patterns of stand structure that appear related to variation in fire regime parameters.

Fire Frequency

In California and southwestern Oregon, fires are known to have been frequent historically in most locations studied (Skinner and Chang 1996, Taylor and Skinner 1998). Median fire return intervals (FRI) for most sites from the southern Cascades, Klamath Mountains, and Sierra Nevada in the foothills, mixed-conifer, eastside pine, and some upper montane areas are generally less than 20 years (McKelvey and others 1996, Taylor and Skinner 1998).

From the perspective of DWM, the variation in fire frequency is probably at least as important as average or median FRI. Fire history studies indicate that before fire suppression it was rare for forested landscapes larger than a few hundred hectares to go for long periods (e.g., > 30 years) without fire (Skinner and Chang 1996, Swetnam 1993, Taylor and Skinner 1998). However, individual sites occasionally experienced longer (several decades) periods without fires severe enough to cause fire scars. FRI variation appears to be related to topography of the landscape (Beaty and Taylor 2001, Taylor and Skinner 1998), elevational gradients (Skinner and Chang 1996), and riparian corridors (Skinner 1997b). Notably, considerable variation in FRI within any given site is often present. These and other factors influencing variation in FRI undoubtedly helped to create diverse and changing patterns of DWM across landscapes. As a result, DWM would probably be clustered both in time and in space and sparsely distributed in the intervening time and space.

Several important patterns of variation appear to be emerging from intensive, landscape-scale, fire-history studies. Two studies in the Klamath Mountains have shown that fires were historically frequent (median FRI <20 yrs) throughout the studied landscapes regardless of tree species composition patterns (Taylor and Skinner 1998).[3] However, variation in fire frequency was found to be associated with slope orientation (aspect) (Beaty and Taylor 2001, Taylor and Skinner 1998) and broad elevational gradients (Agee 1991, Caprio and Swetnam 1995, Taylor 2000). Notably, the variation of FRI within a sample site is often as great or greater than are the differences among sample sites within a particular study. Generally, it appears that FRI is more closely related to a landscape's topographical structure than to the species composition of vegetation.

Although the frequency of past fires is important, it is but one of many factors that define fire regimes. In order to understand how fires may have influenced the dynamics of DWM, there is a need to better understand other characteristics of fire regimes, such as patterns of seasonality and severity.

Severity

Intensive landscape-scale studies in both the southern Cascades and the Klamath Mountains have shown that patterns of fire severity appear to be strongly related to a landscape's topography (Beaty and Taylor 2001, Taylor and Skinner 1998). The pattern that emerged in these studies indicates that slope position and aspect influenced fire severity *(fig. 1)*. Generally, within the local topography, the upper third of slopes displayed the highest proportion of area burned at greater severity, the middle third was intermediate, while the lowest third of the slopes displayed the least amount of severely burned area. When aspect was considered, a higher percent of area burned at higher levels of severity on south and west facing slopes. These are the slopes that are more strongly exposed to afternoon sun and the up-slope winds associated with more severe burning conditions. In contrast, the east and north facing slopes, associated with cooler, more humid conditions, had considerably less area with evidence of severe burns.

Seasonality

Time of year is important for understanding potential effects of fire on DWM. Fires are primarily spread by smaller dead fuels that dry out rapidly following the cool, wet season (Rothermel 1983). Notably, the larger the DWM, the longer it will take to dry out sufficiently to burn (Agee 1993, Martin and Brackebusch 1974). Thus, fires that occur in late summer and early fall are likely to consume more DWM than fires that occur in spring and early summer (Kauffman and Martin 1989).

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[3] Unpublished data for the Hayfork Adaptive Management Area on file at the Silviculture Laboratory, Pacific Southwest Research Station, Redding, Calif.

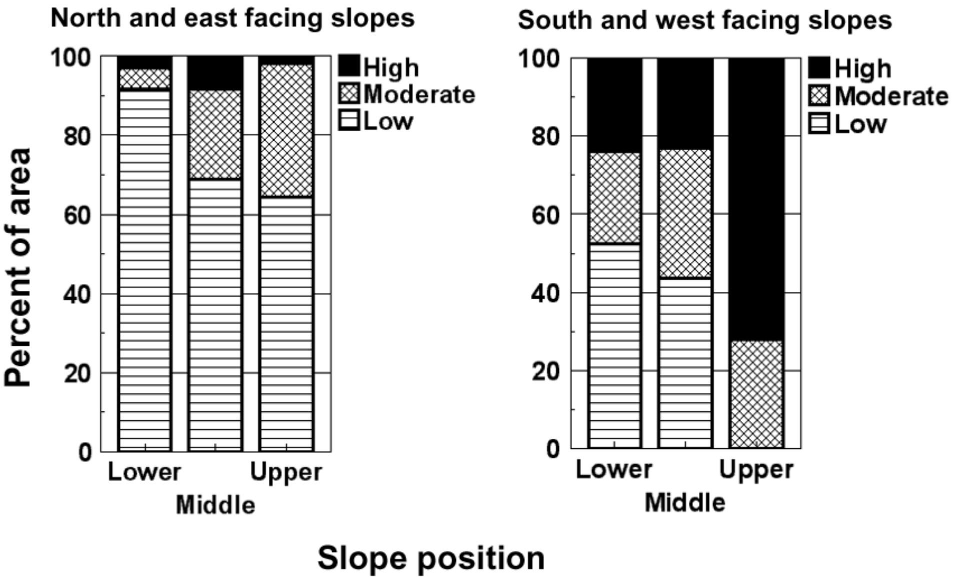

Figure 1—Topographical pattern of historical fire severity found by Taylor and Skinner (1998).

Season of burn may be inferred from the position of the fire scar within a particular tree ring (Caprio and Swetnam 1995). Generally, in California and southwestern Oregon, earlywood scars are interpreted as late spring/early summer fires, latewood scars as midsummer fires, and dormant season fires as late-summer or fall (Caprio and Swetnam 1995, Taylor 1998a, Taylor and Skinner 1998).

Fire history studies from the Klamath Mountains, southern Cascades, and northern Sierra Nevada commonly record the predominance of fire scars in the dormant period *(fig. 2)*. This suggests that most fires occurred in the late summer and fall—the driest part of the fire season and the time of year supporting the most consumptive burns (Thornburgh 1995). In the southern Sierra Nevada most fires were recorded in latewood, suggesting mid- to late-summer fires *(fig. 2)*. Fires burning at this time, while not necessarily at the driest part of the fire season, would also have burned under relatively dry conditions and would have been consumptive.

The likelihood that DWM will be consumed in a fire is related not only to season of the burn, but also to the degree of decomposition. Generally, the more decomposed the wood, the more likely it is to be consumed by fire during the drier portions of the fire season (Kauffman and Martin 1989, Martin and Brackebush 1974). Thus, in southwestern Oregon and California, it is unlikely that much DWM was able to decompose fully before fire suppression was implemented. The annual dry season and the frequency of fire suggest that a major role of fire was to accelerate the removal of DWM from the forests of this region.

It appears that landscape patterns of seasonality may be similar to patterns of severity. South and west facing slopes, especially the upper thirds and ridgetops, often have a portion of fires recorded in earlywood. In contrast, the fire scars found on trees occupying the lower thirds of slopes, especially on east and north facing aspects, are almost exclusively found in the dormant season (Beaty and Taylor 2001).[3] It is unlikely that early-season fires are necessarily more severe. Rather, these data suggest that those places that undergo early drying and can burn early in the fire season are also those that will probably burn more severely later in the season in other years. This is probably a result of more complete drying over the course of the fire season.

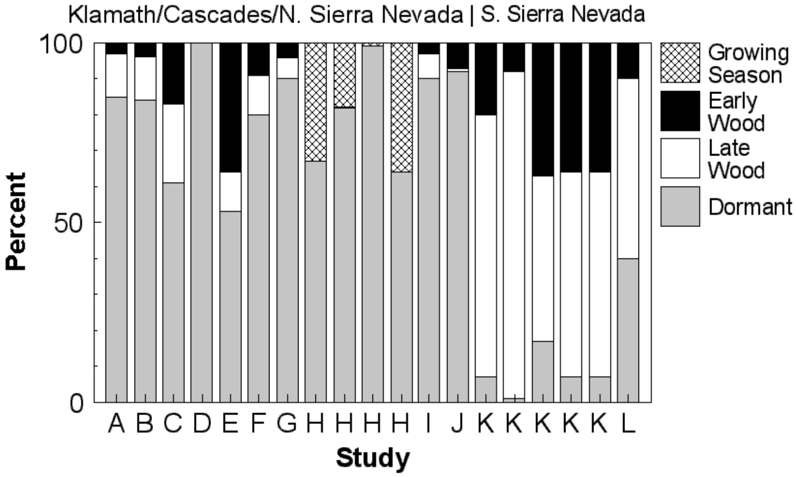

Figure 2—Intra-annual locations of fires scars in fire history studies from the Klamath Mountains, southern Cascades, and Sierra Nevada ranges arranged from north to south. Dormant season scars indicate late summer and fall fires; latewood scars indicate mid to late summer fires; and earlywood scars indicate spring and early summer fires. Where 'Growing Season' is used the study did not differentiate between late and early wood scars. Sources of data: A—Taylor and Skinner (1998); B—Unpublished data for the Hayfork Adaptive Management Area on file at the Silviculture Laboratory, Pacific Southwest Research Station, Redding, Calif.; C—Bekker and Taylor (2001); D—Solem (1995); E—Taylor (1998b); F—Norman and Taylor (1996); G—Norman and Taylor (1997); H—Taylor (2000); I—Beaty and Taylor (2001); J—Taylor (1998a); K—Swetnam and others (1992); L—Caprio and Swetnam (1995).

In climate regions characterized by less frequent fires and significant moisture in the warm season wood is often able to more fully decompose over time. In these more moist climates DWM has been found to be an important factor influencing patterns of nutrient cycling, micro-site moisture regimes, and development of invertebrate and fungal habitats among others (Harmon and others 1986). However, since it is unlikely that much DWM was able to decompose fully under historical fire regimes in the summer-dry climate of this region, very different ecological processes, of which there is only limited understanding today, were operating to influence these same ecological factors.

There are many other factors that may influence the variation of fires as they move across landscapes: fuel loading (often influenced by site quality), weather conditions, past history of fires, riparian corridors, rock outcrops, lakes, and patterns of insect activity and windthrow, among others. The factors that have been discussed in this paper are those that have been found to be important *ipso facto*.

Summary

Before this century, fires in the forests of southwestern Oregon and California were frequent and mostly of low and moderate severity. This was primarily because of the Mediterranean climate that virtually guaranteed a fire season every year regardless of total annual precipitation (as it does today) coupled with ample ignition sources and an absence of fire suppression. As a result, it was rare that any sizable areas would have escaped fire for more than a few decades. The frequency of the fires suggests that it was rare for DWM to have decayed fully before being consumed. Variability in fire regime characteristics has been found to be related to topography of landscapes. This variability probably contributed to variation in the spatial distribution of DWM over time. How past fire regimes would have affected the spatial patterns of accumulations of DWM through time is not yet known and is an important question for future research. Fire history research can help one to understand the variation in fire regimes and their contribution to vegetation patterns. This will help to suggest patterns of stand structures and dynamics that would have influenced spatial and temporal patterns of DWM. At the same time, there is a great need for empirical studies that evaluate the effect of fire on DWM under a variety of burning conditions (Kauffman and Martin 1989) in different landscapes and forests. Long-term experimental studies or adaptive management projects that monitor repeated prescribed burns over time would be especially useful.

Without further research, we will continue to be limited to conjecture in regards to the historical or reference spatial/temporal dynamics of DWM in regions characterized by annual summer drought and frequent fires. To fill the lack of knowledge, we will probably continue to impose standards from forests of other climate types that will carry with them a great deal of uncertainty in terms of the potential to successfully achieve long-term goals in our fire prone environments.

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Demographics and Dynamics in Coastal Mesic Forests

Simulation of Stream Wood Source Distance for Small Streams in the Western Cascades, Oregon[1]

Mark A. Meleason,[2] Stanley V. Gregory,[2] and John Bolte[3]

Abstract

The model, STREAMWOOD, is an individual-based stochastic model designed to simulate the dynamics of wood in small streams of the Pacific Northwest. We used STREAMWOOD to examine source distance as a function of tree fall regime and stand age. Our results suggest that source distance increased with stand age for the first 400 years of stand development and then declined. Simulated source distance for mature conifer forests (81 to 200 years old) were consistent with observed data, but simulated source distances for old-growth forests (201 to 1,000 years old) were below observed data. Further information on stand ages for the forests used in the observational study would refine the compassion with simulated data.

Introduction

One consideration of riparian forest management is the long-term recruitment of wood to the stream. The chance of a riparian tree entering the channel is related to its source distance (Van Sickle and Gregory 1990). We define source distance as the slope distance between the stream bank and the base of the tree perpendicular to the stream channel. Several studies have addressed the relationship between source distance and riparian forest width in the Pacific Northwest. McDade (1987) and McDade and others (1990) surveyed 39 streams adjacent to either mature conifer (80 to 200 years old) or old-growth conifer (> 200 years old) riparian forests in western Oregon and Washington. The source distance for 90 percent of the wood inputs was found to originate within 26 m for mature conifer and 36 m for the old-growth stands. McDade and others (1990) also modeled the source distances for riparian stands composed of uniform heights. The simulated source distance for 90 percent of the trees 40 m and 50 m tall was 32 m and 40 m, respectively.

Van Sickle and Gregory (1990) developed a computer model that simulates the recruitment of stream wood from riparian forests with trees of mixed heights. They applied this model to a mixed-hardwood/conifer stand in the Oregon Cascades and found that 90 percent of the pieces originated within 18 m from the bank. The authors

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also proved mathematically that, for a forest of uniform height, approximately three times as many trees would enter the channel falling directly towards the stream bank as opposed to falling randomly.

These studies provide valuable insights into the relationship between width of the riparian zone and recruitment of wood into a stream. However, these studies give limited insight into how source distance varies with stand age. The purpose of this study was twofold: to compare the results of the simulations reported here with the results from this previous studies and to investigate changes in source distance through time as a function of stand age.

Model Description

We developed STREAMWOOD, a computer simulation model, to investigate the dynamics of wood in streams. (A brief description of STREAMWOOD is provided here; further information can be found at our Web site: http://www.fsl.orst.edu/lter/research/compplfr.htm). STREAMWOOD is an individual-based stochastic model that operates on an annual time step at the reach scale. Stream systems that can be simulated range from a single reach to a small basin. Stream wood dynamics represented in the model are tree entry, breakage, movement, and decomposition. Riparian forest inputs are generated either from a simplified forest gap model built within STREAMWOOD or from a user-specified input file. The model is run under a Monte Carlo procedure and the results are reported as average conditions per reach. The current version of STREAMWOOD was developed for fifth-order and smaller streams in the coniferous forests of the Pacific Northwest. Species considered include Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco), western hemlock *(Tsuga heterophylla* [Raf.] Sarg.), western red cedar *(Thuja plicata* Donn ex D. Don), and red alder *(Alnus rubra* Bong.).

The forest model within STREAMWOOD was based largely on three existing forest–gap models: ZELIG (Pacific Northwest version by Steven Garman, Forest Science Laboratory, Corvallis Oregon), JABOWA (Botkin 1993, Botkin and others 1972), and CLIMACS (Dale and others 1986, Dale and Hemstrom 1984, Hemstrom and Dale 1982). Since the forest model adheres closely to the original design of Botkin and others (1972) and Shugart (1984), it inherits many of their limitations (Schenk 1996).

Riparian Zone Definition in STREAMWOOD

A simulated stream reach consists of a length, bankfull width, and a riparian forest adjacent to each bank. The dimensions of each riparian forest is the reach length by a width selected between 0 m to 100 m. A tree fall regime is associated with each riparian forest. In a random fall regime, trees have an equal chance of falling in any direction. In a directional fall regime, tree fall angle is normally distributed around a mean (and standard deviation) fall angle. A directional fall regime defined with a mean of 180 degrees and a standard deviation of zero forces all trees to fall directly towards the channel.

Initial Conditions

We conducted two simulations with STREAMWOOD using the forest model to grow identical riparian forests. Both simulations were run for 1,000 years and 200 iterations. In the first simulation, trees could fall in any direction (random fall), and in the second all trees were forced to fall directly across the channel (directional fall). Both simulations represented riparian forests in the Oregon Cascades at an elevation of 300 m. Soil moisture content was set such that the growth of red alder was negligible, but supported Douglas-fir, western hemlock, and western red cedar. The reach dimensions were 100 m long and 15 m wide. The thermal growth index was set at 1,500 growing degree-days (5.5ºC base) with a standard deviation of 100 growing degree-days.

The simulated riparian forests were 75 m wide and started with no trees. The riparian forest was divided into 31 intervals, or source distances, parallel to the stream bank. The first 30 intervals were 2 m wide, and the last interval was for recruitment of all pieces ≥ 60 m from the bank. For each source distance, the mean number of input events that entered the channel during each 10-year period was calculated. An input event included any tree that contributed a piece at least 10 cm top diameter and 1 m in length to the stream.

Results and Discussion

Comparison with Previous Studies

The first purpose of this study was to compare the results from the simulations with the results of previously published studies. Van Sickle and Gregory (1990) proved mathematically that, given a stand composed of trees of the same height, exactly 1/л less input events would result from trees falling randomly as opposed to falling directly across the channel. We extend this proof to stands composed of mixed heights. Consider a riparian forest containing trees of two different heights. The ratio of input events between random and directional fall would be identical (1/л) for both heights. The ratio for the entire stand would also be 1/л since it is the sum of all random fall inputs over the sum of directional fall inputs. Extending this argument, the ratio of 1/л would hold for any number of height classes.

The input ratio described by Van Sickle and Gregory (1990) provided a simple test for evaluating STREAMWOOD's performance. The two simulations reported had identical initial conditions except for the fall regime used. The ratio of the number of input events from the two simulations was determined *(fig. 1).* The mean ratio between the number of input events from random and directional fall was 0.307 with a standard deviation of 0.018. The mean input ratio from the simulations was 3.6 percent lower than the predicted value and could be due to small differences between the two simulated forests. The coefficient of variation was 5.8 percent and most likely could be reduced with an increase in the number of iterations. Thus, the performance of the model was consistent with the predictions of Van Sickle and Gregory (1990).

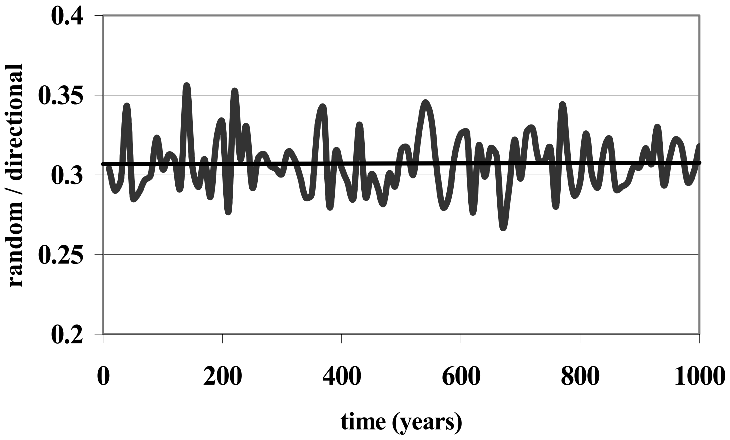

Figure 1—Ratio of input events from random and directional fall. The mean ratio of input events for each 10-year period was determined using the two simulations. The global mean obtained over the 1,000-year simulation was 0.31 (solid line). This value is consistent with the expected value of 0.32 (Van Sickle and Gregory 1990).

The second comparison with previous work was with the source distance estimates presented in McDade and others (1990) *(fig. 2, table 1).* The old-growth curve from McDade and others (1990) lies entirely below both source distance curves from this study, while the majority of the mature conifer curve lies between the source distance curves from this simulation. In addition, both source distance curves from McDade and others (1990) were very similar for the first 5 meters and below either of the simulated source distance curves.

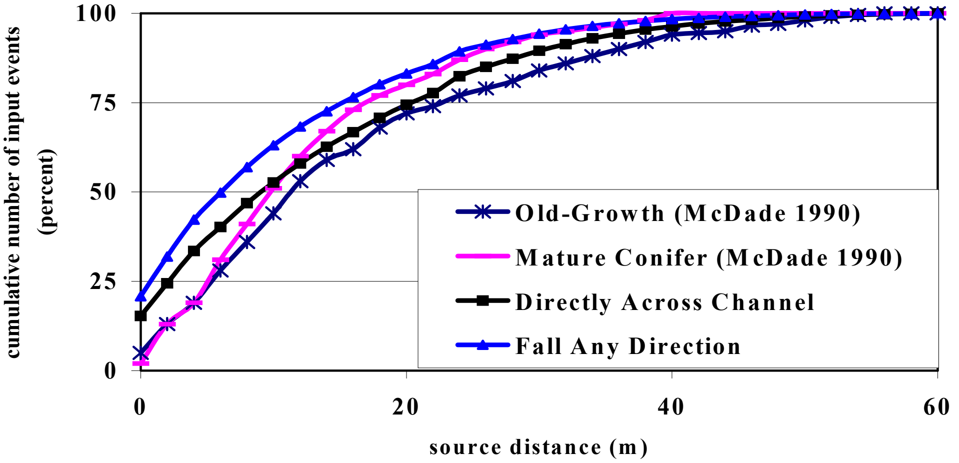

Figure 2—Comparison of source distances, western Cascades, Oregon. The two source distance curves from this study are compared with those presented in McDade and others (1990). The simulated source distance curves include all input events over a 1,000-year period. The simulated random fall curve is consistent with observed mature conifer curve, but the observed old-growth curve is greater than both simulations.

Table 1—*Comparison of source distances between the two simulations and data in McDade and others (1990). Two source distances are reported for each forest age class. These distances represent 50 and 90 percent of the input events associated with a forest age class.*

Study	Forest age class (years)	Source distance (m)	
		50 percent	90 percent
McDade (1990)	81 – 200	10	26
	> 200	12	36
Random fall	All Ages	6	26
(this study)	≤ 80	3	14
	81 – 200	8	26
	201 – 400	6	30
	> 400	6	24
Directional fall	All Ages	10	31
(this study)	≤ 80	4	20
	81 – 200	12	32
	201 – 400	10	36
	> 400	9	30

Possible explanations for the discrepancies in source distance between the results of McDade and others (1990) and the simulations may be related to the biases inherent in each approach. The tree fall regimes in the study sites surveyed may not be completely random. Thus, it would be expected that the source distance curve for the old-growth would lie between the random and directional source curves. In the simulations, the density of trees within the plot was assumed uniform. However, tree densities in the field plots surveyed by McDade and others (1990) may not be uniform, especially within the first few meters from the stream bank. The region adjacent to the stream bank is more susceptible to disturbance from high flows and typically has higher light levels reaching the forest floor—conditions favoring the establishment of early successional species.

The cumulative percent of input events for the first 2 meters was substantially less in the field study (2 and 5 percent) than in the simulations (15 and 21 percent). This difference suggests that the number of input events close to the stream bank was overestimated by STREAMWOOD. However, the simulations accounted for all input events that occurred over a 1,000-year period. In contrast, since the persistence of input events is not equal, larger and more recent events would be favored in the field surveys. Most likely, the cumulative percent of inputs 2 m and less from the channel are between the field and simulation estimates.

Source Distance and Stand Age

The second objective of this study was to investigate how cumulative input of wood into a stream varies through time as a riparian forest matures. Maximum source distance is equivalent to the maximum effective height (height to 10 cm top diameter) for a given species. In STREAMWOOD, the maximum effective height for the three species used in the simulation are approximately 80 m for Douglas-fir, 60 m for western hemlock, and 55 m for western red cedar. As noted previously, the riparian zone was divided into 30 source distance sub-zones 2 m wide, and one additional category for all input events occurring > 60 m from the stream bank. In our simulations, trees obtained sufficient height in approximately 450 years to contribute stream wood 60 m from the channel.

The source distance associated with 90 percent of the input events as a function of stand age was determined for both simulations *(fig. 3).* The maximum value for both simulations occurred between stand ages of 200 to 400 years: 40 m for directional and 34 m for random fall. The source distances reflect the initial dominance of Douglas-fir (200 to 400 years) followed by the eventual dominance of western hemlock *(fig. 3).*

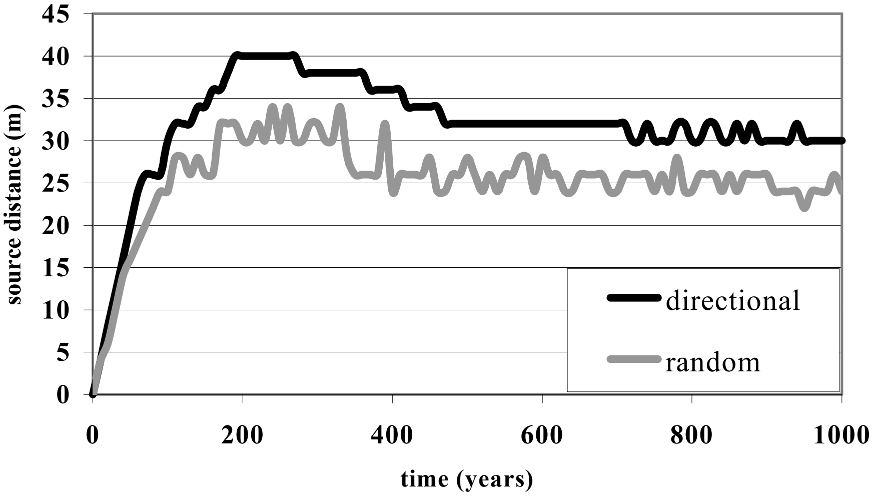

Figure 3—Source distance for 90 percent of the input events from directional and random fall through time. The greatest source distance is associated with a riparian forest dominated by the tree species with the greatest height, Douglas-fir. As the stand matures, Douglas-fir is eventually replaced by western hemlock.

To investigate how source distance varies by stand age, cumulative input events were determined for each of four riparian forest age classes: young conifer (0 to 80 years old), mature conifer (81 to 200 years old), Douglas-fir dominated old-growth (201 to 400 years old), and hemlock dominated conifer (> 400 years old) *(figs. 4, 5; table 1).* Results were similar for both runs *(figs. 4, 5),* with young conifer stands having the shortest source distance, Douglas-fir dominated old-growth stands having the longest source distance, and the mature conifer and western hemlock dominated old-growth having almost identical source distances. The difference between the two runs can be illustrated by comparing the source distance at the 50 percent and 90 percent cumulative input levels *(table 1).* At the 50 percent level, the source distances for all forest age classes, save for the young conifer, were within 3 meters. For the 90 percent level, the three older forest age classes were within 6 meters.

Finally, comparisons were made between the simulation results of the mature conifer *(fig. 6)* and old-growth stands *(fig. 7, table 1)* with those of McDade and others (1990) *(fig. 2).* For the mature conifer age class, source distances ≥ 14 m were almost identical between the field survey and the random fall simulation *(fig. 6, table 1).* This suggests that trees tend to fall randomly in the interior of the stand. This warrants further testing.

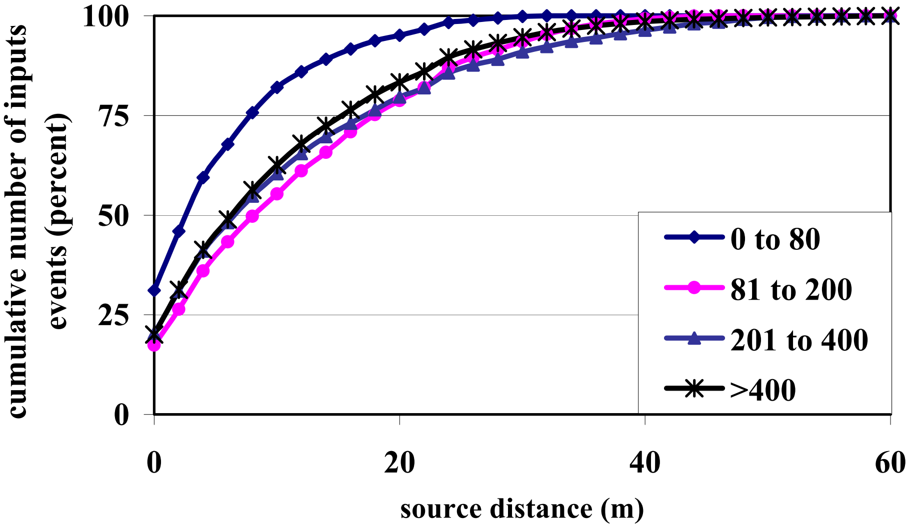

Figure 4—Cumulative number of input events from random fall as a function of the riparian forest age class. The four forest age classes represent young conifer, mature conifer, old-growth dominated by Douglas-fir, and old-growth dominated by western hemlock.

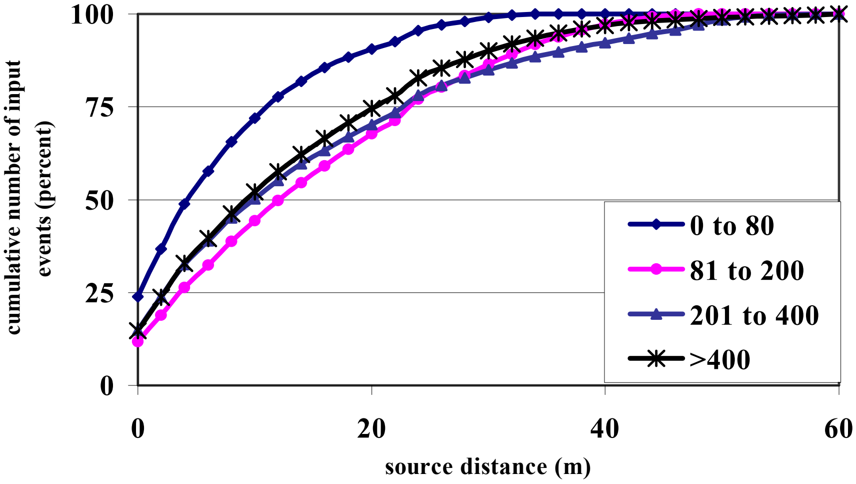

Figure 5—Source distance for the directional fall simulation as a function of the riparian forest age class. The four forest age classes represent young conifer, mature conifer, old-growth dominated by Douglas-fir, and old-growth dominated by western hemlock.

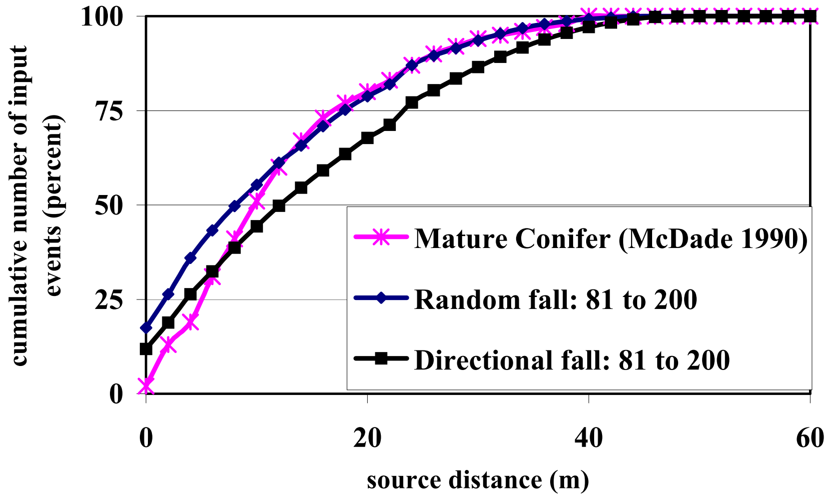

Figure 6—Comparison of source distance estimates for mature conifer, western Cascades, Oregon. Comparison of mature conifer source distance curves from the two simulations and McDade and others (1990). Each simulated source distance curve includes only those input events from stand ages between 81 to 200 years. The random fall source distance is consistent with the observed for source distances ≥ 14 m. This suggests that in the surveyed plots, trees ≥ 14 m from the stream bank tended to fall in any direction.

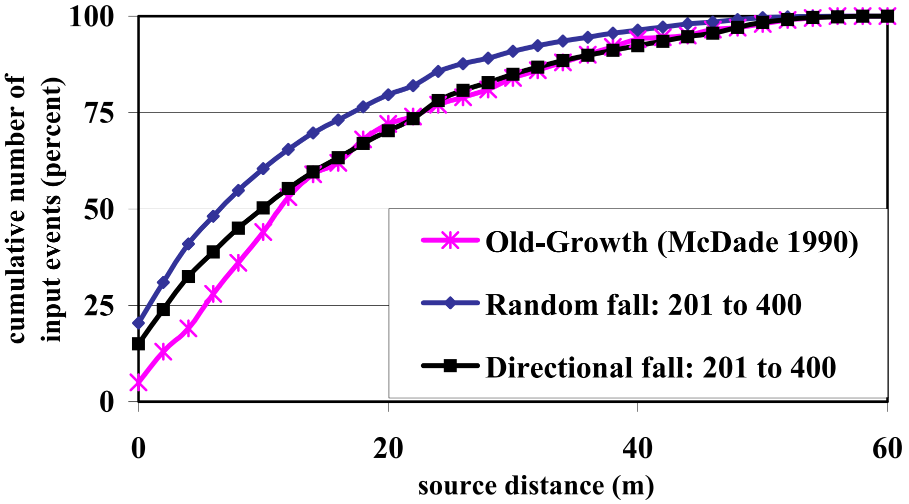

Figure 7—Comparison of source distance estimates for old-growth conifer, western Cascades, Oregon. Comparison of old-growth source distance curves from the two simulations and McDade and others (1990). Each simulated source distance curve includes only those input events from stand ages between 201 and 400 years. The directional fall source distance is consistent with the observed for source distances ≥ 14 m. This suggests that in the surveyed plots, trees ≥ 14 m from the stream bank tended to fall directly towards the channel, which is unlikely. The forest age-class of 201 to 400 years old may not be the appropriate age class for this comparison. Further information on stand ages of the surveyed plots is needed to construct an appropriate comparison.

For the old-growth age class between 201 and 400 years, source distances ≥ 14 m were almost identical to the field surveys and the directional fall simulation *(fig. 7, table 1).* This would suggest that trees of this age class tend to fall directly towards the channel, which is highly unlikely. However, the source distance curves appear to be sensitive to the definitions used for the forest age classes. Evidence for this can be found by comparing the simulation results *(fig. 2),* which includes all input events over the 1,000-year period, with the simulation results divided by forest age class *(figs. 6, 7).* Note that both the directional and random source curves have shifted down with respect to the mature and old-growth curves from McDade and others (1990).

The majority of input events identified in a field survey may be associated with the recent history of the forest stand. The close agreement with the mature conifer age class may be attributed in part to a well-defined forest age class. In contrast, the old-growth age classes used to classify the simulation results may not be equivalent to the old-growth stands surveyed by McDade and others (1990). Further information on stand age of surveyed sites would be necessary to define appropriate forest age class to use in this comparison.

Conclusion

Van Sickle and Gregory (1990) provided a mathematical proof that approximately one-third as many trees would enter the stream falling in any direction than falling directly across the channel. The results of this study were found to be consistent with this ratio. McDade and others (1990) found that 90 percent of the input events occurred within 26 m and 36 m from the stream bank for mature conifer and old-growth respectively. Over the entire 1,000-year simulation, 90 percent of the input events occur within 26 m and 31 m for the random and directional fall, respectively. A closer agreement between the two studies was found after accounting for stand age *(table 1).*

Large wood in streams is an important component in a stream ecosystem. One goal in managing riparian forests is to ensure the long-term supply of wood to the stream. The results from this study suggest that source distance varies with stand age. Based on a 1,000-year simulation, the largest source distance occurred with stand ages between 200 and 400 years old *(fig. 3).* These results may be useful in determining the appropriate riparian buffer width to ensure an adequate supply of wood to a stream. However, the recruitment of wood to streams is only one of many criteria that should be considered when developing management plans for riparian forests and the protection of the stream ecosystems.

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Standing Dead Tree Dynamics Extracted from Growth and Yield Permanent Sample Plots in British Columbia[1,2]

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Abstract

Permanent sample plots established to study the growth and yield of live trees can provide valuable information on standing dead tree dynamics. Even if dead trees were not traditionally measured, a subsequent measurement of dead trees enables extraction of information on past dynamics. In British Columbia (BC), Canada, the Ministry of Forests administers over 5,500 growth and yield permanent sample plots that could provide important information on dead tree dynamics. In this paper we discuss the standing dead tree information obtainable from these plots, the time needed for and costs of measuring, and current findings on standing dead tree dynamics in BC.

Introduction

In British Columbia (BC), Canada, the ecological value of wildlife trees (i.e., standing dead trees and defective live trees) is well recognized within forest management and operational practices. The BC Wildlife Tree Committee, established in 1985, has worked to improve the conservation of wildlife trees while addressing the legislative needs for safety in forest operations. Legislation and associated guidelines under the Forest Practices Code of British Columbia Act identify and require the conservation of wildlife trees through reserve and management zones.

Knowledge and tools about the dynamics of standing dead trees (e.g., fall rates) can assist forest managers with decisions at the tree level (e.g., safety concerns of individual trees) to the landscape level (e.g., characteristics of wildlife tree patches). These dead tree decisions can influence and are influenced by decisions made for other resources including timber and wildlife. Tools to assist dead tree decisions must be integrated with both traditional forest management tools for timber values (e.g., growth and yield models) and for non-timber values (e.g., habitat suitability indices). However, basic information on the dynamics of standing dead trees that would enable

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

[2] This paper reflects government organization, legislation, or policy as of December 1999.

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appropriate projections for forest management and silvicultural planning is generally lacking.

Backhouse and Lousier (1991) and Caza (1993) noted the potential of BC's extensive growth and yield (GY) permanent sample plot (PSP) program to provide information on dead tree dynamics. A GY PSP is typically a fixed area in which trees of a minimum size are permanently marked and regularly remeasured at a fixed interval between 2 and 10 years. Minimally, the individual trees are measured for species, diameter at breast height (DBH), and a few other characteristics. On a subset of trees, more detailed measures such as height and age may be included. On more intensive PSPs, the location of individual trees will be recorded and each tree will be measured in greater detail.

In BC and elsewhere, GY PSPs have historically provided information only on the live tree dynamics of forest stands. The measurement of a tree typically stopped at its death. With increased ecological concerns, the continued monitoring of a tree past its death is now a more common practice. Fortunately, the repeated measures nature of a PSP enables some of the past dynamics to be extracted immediately upon the first measurement of standing dead trees in an existing plot.

The initial measurement of standing dead trees on an established GY PSP creates a cohort data set of standing dead trees identified as dead in each of the past remeasurements. These data can be analyzed or modeled by many methodologies—some more appropriate than others. The data may be fit to a negative exponential decay function, and general decay (i.e., fall rates) can be reported (Harmon and others 1986). A life-table or transition matrix approach can be used to present rates of fall (Huggard 1999, Krebs 1978, Raphael and Morrison 1987). Lee (1998) extracted the dynamics of fall for aspen trees in Alberta with failure analysis techniques on a large PSP data set. Logistic regression models have also been used to predict dead tree fall both at the tree and stand levels (Raphael and Morrison 1987, Stone 1996).

Standing dead trees provide a link between forest stands and many animal habitat/population dynamics. Standing dead tree models have been structured to enable input from forest stand growth and yield models and provide output useful for habitat/population models (Raphael and Morrison 1987). Marcot (1992) directly linked the fall model, Snag Recruitment Simulator, with habitat requirements of woodpeckers (Ohmann and others 1994, Schuster and others 1993). Fall models built into growth and yield models such as Tree and Stand Simulator (TASS) (Mitchell 1975, Stone 1996) or as extensions such as the Forest Vegetation Simulator Fire and Fuels Extension (Beukema and others 1997) have been linked to habitat suitability type models to look at the impacts of direct management regimes (Greenough and Kurz 1996, Greenough and others 1999). Standing dead tree models are not limited to fall dynamics only. They may provide other characteristics, such as decay stage, important to habitat linkages (Huggard 1999, Raphael and Morrison 1987).

Underlying the usability of any standing dead tree model are the basic data of dead tree dynamics. In this paper, we discuss the information about standing dead trees currently collected on GY PSPs in BC and further describe an example of standing dead tree data from one of BC's earliest growth and yield sample plots. We note that our viewpoint is primarily from the perspective of the Ministry of Forests' Growth and Yield programs and might not reflect other programs (e.g., those of the forest industry).

PSP Dead Tree Measurement in British Columbia

The BC Ministry of Forests (MOF) has an extensive GY PSP program (> 5,000 PSPs), typically establishing and remeasuring between 200 and 700 plots annually. The earliest PSPs were established as part of research studies in the 1920s, although much of the PSP program was established after the 1960s:

Period	Number of PSPs established[1]
1920-39	90
1940-49	487
1950-59	319
1960-69	2,163
1970-79	1,528
1980-89	994
1990-97	1,412

[1] The number of PSPs shown represent those maintained by the Ministry of Forests, Resources Inventory Branch.

GY PSPs are established and remeasured by several programs within the MOF. The Resources Inventory Branch (RIB) administers the largest program that is conducted through regional offices. These PSPs tend to be in unharvested rather than treated forests. Researchers from Research Branch and Regional Offices maintain PSPs within research installations and silvicultural systems trials that have a wide range of research objectives and treatments. Industry and academia also have established PSP programs adding over 4,000 PSPs to the provincial PSP program.

The Forest Productivity Council (FPC) of BC—whose members are from government, industry, and academia—has taken a lead role provincially to coordinate PSP establishment and remeasurement. The FPC maintains a matrix of forest stand conditions in which existing PSPs in BC are located, thus enabling the determination of where best to place new PSPs. The FPC also maintains provincial minimum standards for GY PSP installation and measurement that are mostly followed by government and industry.

Information collected on dead trees has changed from early PSP establishment in the 1920s to the present. Early PSP measurements may have identified simply that a tree had died. This was later modified to some indication of the merchantable condition of a tree at death through the use of a standardized “tree class” measure assigned to a tree on each remeasurement. Three of the six tree classes concern dead trees: cut (removed by human activity); dead potential (>50 percent sound wood by volume and > 10 cm DBH and 3 m height or length); and dead useless (not cut or dead potential). As interest in dead trees increased in the 1990s, further information on dead trees has been collected within the MOF RIB GY PSP program. In 1991 a tally of standing dead trees by DBH size class was added to the establishment procedures. In 1994, a measure indicating whether a tree that had recently died was standing or fallen was added, as it was not previously possible to differentiate this. These data provided information on dead tree recruitment and inventory at plot establishment. However, little information on dead tree dynamics could be obtained as trees were not revisited after being recorded dead.

In the mid-1990s, several organizations started using GY PSPs to obtain information on dead tree dynamics in BC. In 1993/94, the BC MOF Research Branch initiated the collection of information on standing dead trees from a limited number of PSPs in research trials to determine basic fall rate information *(table 1)*. Wells (1996) analyzed a subset of PSPs of MacMillian Bloedel Ltd. in coastal western hemlock forests to investigate developmental trends of stand structure and tree mortality. Large silvicultural systems trials were initiated during this period in which PSPs were installed and dead tree information was collected (Holstedt and Vyse 1997). Further during this time period, wildlife/danger tree assessment was initiated and standing dead trees were included in new resource inventory standards (Stone and others 2002).

Table 1—*British Columbia Ministry of Forests research trial growth and yield permanent sample plots on which standing dead trees have been measured.*

Research Trial	Treatment	Species[1]	Number of PSPs	Date established	No. of measurements	Date of first dead tree measure
Aleza Lake EPs	Residual cutover	Se, Bl	17	1926-1936	7-9	1998
EP364	Commercial thinning	Fd	12	1950	8	1996
EP368	Species trial	Fd, Hw, Cw, Bg, Ba, Ss, Co	49	1958	7	1998
EP370	Partial cutting	Pw, Hw, Lw, Fd	20	1957	6	1994
EP384/385	Thinning	Pl	12	1953	7	1994
EP388	Commercial thinning	Hw	20	1953	5	1997
EP429	Espacement	Fd, Cw, Bg	18	1963	6	1999
EP534	Juvenile spacing	Fd	46	1959-1963	8-11	1995
EP554	CCT trial	Fd	47	1959	9-11	1997
EP571	Espacement	Fd, Cw, Ss, Hw	157	1962	5-8	1998
EP703	Thinning/ fertilization	Fd, Hw	940	1971-1975	8	1994-2000
EP1065	Pruning	Hw, Cw, Fd	102	1990-94	3	1997-1998
EP1097	Thinning/ fertilization	Hw	36	1992	2	1996
EP1177	Biosolids	Fd	32	1992	4	1998

[1] Ba: Amabilis fir *(Abies amabilis),* Bb: Subalpine fir *(Abies lasiocarpa),* Bg: Grand fir *(Abies grandis),* Co: Port-Orford-cedar *(Chamaecyparis lawsoniana),* Cw: Western red cedar *(Thuja plicata),* Fd: Douglas-fir *(Pseudotsuga menziesii),* Hw: Western hemlock *(Tsuga heterophylla),* Lw: Western larch *(Larix occidentalis),* Pl: Lodgepole pine *(Pinus contorta),* Se: Engelmann spruce *(Picea engelmannii)* Ss: Sitka spruce *(Picea sitchensis).*

Despite the above initiatives, the need for broader information on standing dead tree dynamics was identified by BC dead wood experts (Stone 1997). Measuring standing dead trees within the provincial GY PSPs was potentially an economical method to obtain such information. To determine the feasiblity of this need, the FPC through the MOF RIB conducted a pilot study in 1998 to investigate the cost of including dead tree measures as a minimum GY PSP standard (Forest Productivity Council 1999). We discuss this pilot study later. As a result of the study, the FPC added standing dead tree measures to provincial GY PSP standards and the MOF RIB GY program commenced measuring standing dead trees in the fall of 1999. A review of the standards and the use of the information will be conducted in 2001.

Example Data

In August 1927, George H. Barnes established a 0.405 ha (1 acre) permanent sample plot (this permanent sample plot was originally identified as EP [Experimental Plot] 82 and is currently identified as 6-01L-2R by the Resources Inventory Branch, Ministry of Forests, Victoria, BC) in an unmanaged stand in the municipal Mount Douglas Park (Saanich, British Columbia). Over the past 70 years, the BC MOF has measured this PSP 10 times for tree species, DBH, and selected heights and ages of live trees until their death *(table 2)*. Currently the PSP is predominantly Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) with a small component of big-leaf maple *(Acer macrophyllum).*

Table 2—*The number of live Douglas-fir stems per plot on Mt. Douglas Park (Saanich, British Columbia) growth and yield permanent sample plot. The plot size is 0.405 ha (1 acre). The site index is 27 m @ 50 years (Bruce 1981).*

			Trees per plot by DBH (cm) class				
Measurement year	**Stand age**	**Stems (>7.5 cm) per plot**	**<20**	**20-30**	**30-40**	**40-50**	**50+**
1927	70	282	40	130	73	29	10
1933	76	262	28	117	66	40	13
1937	80	247	25	106	64	45	17
1943	86	222	14	76	62	48	27
1947	90	208	5	63	50	52	38
1953	96	195	4	50	46	44	51
1957	100	195	4	49	45	42	55
1967	110	174	1	30	41	31	71
1977	120	163	1	23	36	18	85
1987	130	154	0	15	33	18	88
1997	140	154	1	15	29	18	91

In the fall of 1998, all standing dead trees (> 1.3 m height) were recorded on the PSP. The individual trees were identified either by the presence of a tag or by comparison with the information for trees known to have died. The height (ocular estimate) and several characteristics (e.g., bark presence, wood condition, branch condition) were measured for each tree. In the description below we discuss only Douglas-fir dynamics. Other conifers are a minor component of this stand. Hardwoods were not included in the PSP measurement until 1987.

Data such as found on this PSP may be analyzed and presented in several formats. A raw summary of the 10 cohorts (based on the number of years since the tree's death was recorded) shows some common features of this type of information *(table 3)*. We note that the size distribution of the dead trees lags behind the size distribution of the live tree dynamics (i.e., trees that die are usually growing slower), and no dead trees have been standing longer than a certain age (i.e., 60 years in this data set). These data can also be graphed as survival curves *(fig. 1)*. Studies such as Harmon and others (1986) report the decay rate derived from simple negative exponential models. For Mt. Douglas data we find a decay rate of 0.035 per annum (standard error [s.e.] = 0.007) for dead trees in the 21-30 cm dbh range. Similarly, the data could be fit to a logistic regression model (Raphael and Morrison 1987). One such fitted model for the Mt. Douglas data is Prob[yrs,DBH] = 1/(1+ EXP(-0.459 + 0.046*yrs – 0.028*DBH)) where Prob[yrs,DBH] is the probability that a dead tree with a given diameter (DBH in cm) will be still standing after x years (yrs).

Table 3—*The number of Douglas-fir stems per plot on Mt. Douglas Park (Saanich, British Columbia) growth and yield permanent sample plot that had died since the previous measurement and the number of dead Douglas-fir that remain standing in 1998. The plot size is 0.405 ha (1 acre). Values in parentheses indicate trees that were cut and thus excluded from fall calculations. A dead standing tree must be at least 1.3 m tall.*

Measurement year	Number of trees in plot that died since previous measurement period by DBH (cm)				Years since death recorded	Number of standing dead trees still standing in 1998 by period of death and DBH (cm)			
	<20	20-30	30-40	40-50		<20	20-30	30-40	40-50
1927	0	0	0	0	71	0	0	0	0
1933	11	8 (1)	0	0	65	0	0	0	0
1937	3 (5)	3 (5)	0	0	61	0	0	0	0
1943	5 (4)	13 (1)	0	(1)	55	2	4	0	0
1947	5	9	0	0	51	2	2	0	0
1953	1	9	3	0	45	1	3	1	0
1957	0	0	0	0	41	0	0	0	0
1967	2	15	3	0	31	0	7	0	0
1977	0	8	2	0	21	0	2	1	0
1987	1	6	3	0	11	0	3	2	0
1997	0	8	9	0	1	0	5	7	0
1998	0	0	1	0	0	0	0	1	0

However, as is well recognized, the robustness and interpretation of the results of any method is dependent upon the underlying data and how they were obtained. These Mt. Douglas data provide a small data set, probably insufficient for most analyses including the above, and are from a single site that would unlikely be representative of a larger population of interest. Appropriate sampling schemes should be employed or, alternatively, a good understanding of the potential biases is needed if the results are to be applied for management purposes.

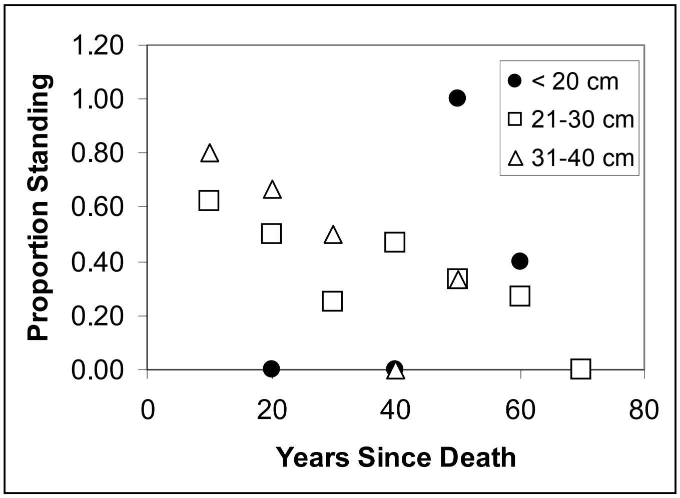

Figure 1—The proportion of dead Douglas-fir stems still standing in 1998 by age group (i.e., years since death) on the Mt. Douglas PSP. The data have been grouped into 10 year periods.

Time Trial

To estimate the cost of obtaining dead tree information within the Ministry of Forests' GY PSP program, we conducted a pilot study (Forest Productivity Council 1999). Nine existing plots that covered a range of characteristics in terms of stand density, age, and time since establishment were chosen. Four plots were located in the Kamloops Forest Region of interior British Columbia and five plots in the Vancouver Forest Region of coastal British Columbia. On each plot, all standing dead trees were located and measured for a variety of characteristics. These measures included base (e.g., standing or fallen, height to breakage, wildlife tree appearance) and special informational needs (e.g., bark condition, lichen loading), as identified in a needs assessment by 44 individuals interested in dead tree data in British Columbia (Stone 1997).

The time study found that for the base set of measures (species if needed, DBH if needed, tag identification if needed, vertical position [standing or fallen], breakage, height to break if needed, and wildlife tree visual appearance), the average time required per tree was 51 seconds (s.e. = 2.0). For the typical tree (i.e., has a tag and does not require DBH or species), the average time required to collect these base measures was 19 seconds (s.e. = 0.7).

The PSPs in the pilot study were selected to sample a range of conditions, not to be representative of the entire sampling program. The average number of dead trees per plot of the MOF PSP sampling program is expected to differ from the average of the pilot study. To determine an estimate of the standing dead trees that might be found on an average MOF PSP, we randomly selected 100 PSPs with at least two remeasurements (i.e., 20 years since establishment) from the active provincial sampling program. From these 100 PSPs (mean size 0.087 ha), we obtained an average of the expected number of trees over 10 cm DBH at a remeasurement (8.6 per plot, s.e. = 0.72) that died since the previous measurement. We then estimated that 10.7 (s.e. = 0.79) trees per plot that died before the previous measurements would still standing. The latter was estimated by applying, as a best guess, a logistic fall model for Douglas-fir to tree mortality information in each PSP (Stone 1996).

We were interested in the incremental costs of measuring all standing dead trees during the regular PSP remeasurement. If we assume that the 1998 average contracted bid price for plot measurement in the MOF GY PSP program was $1,000 for 10 hours per plot, we find that the inclusion of the base measures for dead trees greater than 10 cm DBH added $29 to $39 to the cost of measurement. This low cost was also reflected in the MOF Research Branch coastal research PSP program. In the second year of the collection of dead tree measures in 1997, accepted bid prices were similar to those in 1993 for the same plots when no dead tree measures were collected (de Montigny 1998). However, in the initial year of the collection of dead tree measures, an increase in bid cost did occur probably due to the uncertainty among contractors about the costs of dead tree measures.

Use of PSP Data in BC

Dead tree information needs in British Columbia have been identified in various reviews (Backhouse and Louiser 1991, Caza 1993, Lofroth 1998, Machmer and Steeger 1995). These needs can be summarized into four categories: the development of policy and management guidelines; understanding the ecological role of dead trees; understanding the status and dynamics of dead trees; and operational forest management (Stone 1997). Most uses of dead tree information in current forest management practice (e.g., wildlife/danger tree assessment, residue and waste surveys, wildlife tree patch determination and mapping) involve a static field identification of dead wood resources. However, most of the identified needs require information on the dynamics of dead trees and the linkages to their ecological roles.

Information from PSPs can satisfy many of the basic needs on dead tree dynamics. Simple summaries of fall rate information by species and forest type will provide insight for researchers and forest managers needed for developing prescriptions related to wildlife tree reserves. Fall and breakage rates in relation to live and dead tree conditions can assist in assessing wildlife/danger tree assumptions. Data from the MOF PSP program are publicly available. Researchers might make use of the PSPs to collect further non-destructive measures to address specific information needs (e.g., decay development, bark sloughing) and potentially correlate these to the larger PSP information base.

The primary identified use of the raw data from the MOF GY PSP program will be for the development of empirical models of dead tree fall included within the MOF growth and yield models TASS, TIPSY, and PrognosisBC (for description of the models, see http://www.for.gov.bc.ca/research/gymodels). TASS is an individual tree distance-dependent growth model that is currently suitable for modeling BC's major commercial species in single species even-aged stands (Di Lucca 1999, Mitchell 1975, Stone 1996). The model enables silvicultural treatments such as thinning, fertilization, and pruning and has a wide array of outputs. However, the model is not publicly distributed. TIPSY is a publicly distributed model that interpolates yield tables derived from TASS. TIPSY has a limited set of silvicultural options but provides a wide range of growth and yield outputs as well as economic summaries. PrognosisBC is a BC derivative of the Forest Vegetation Simulator

(FVS) that has been parameterized for use in several ecosystems of southeastern BC (Robinson 1997).

The empirical dead tree fall models currently used in TASS and TIPSY are logistic models derived from a limited number of PSPs in BC for Douglas-fir, western hemlock *(Tsuga heterophylla),* and lodgepole pine *(Pinus contorta) (table 4)*. Other species either use Douglas-fir parameters as a default or have been modified to reflect a perceived relative rate of fall as compared to Douglas-fir. The logistic models used time since tree death and DBH at death as the independent variables. While both TASS and TIPSY use logistic models, they are applied in different manners. In TASS the models are applied to individual trees and if the probability of fall is greater than a randomly assigned value, the tree is considered to have fallen. In TIPSY the models are applied to stand level information (average DBH class and time since death) and the probability is treated as the percentage of the number of trees in that class that will have fallen during a time period. These fall models will be reparameterized as new data become available. Furthermore, the dead tree model structure in TASS is also expected to change to reflect greater biological/mechanical relationships.

Table 4—*Standing dead tree logistic fall models incorporated as default parameters within dead tree fall models of the Ministry of Forests' growth and yield model TIPSY. The model is ProbStanding = 1/(1+ EXP(b0 + b1*YearsSinceDeath + b2*DBHatDeath)). Only non-treated plots dominated by the species of interest were used.*

Source	Establishment date	Dead tree measurement date	No. of PSPs	DBH range (cm)	Species	Standing dead trees	Total trees died since establishment	b0	b1	b2
EP703[1]	1971-75	1994-95	46	4.2 - 54.6	Fd	1,518	3,986	-1.369	0.132	-0.063
EP703[1]	1971-74	1994-95	16	4.9 - 48.8	Hw	1,063	2,137	-2.094	0.169	-0.057
EP384/85[2]	1953	1994	2	3.3 – 26.9	Pl	28	255	0.662	0.146	-0.074

[1] EP703 consists of 940 PSPs located at 85 installations on Vancouver Island and the coastal mainland of British Columbia (Darling and Omule 1989, Stone 1996). Species composition of these PSPs varies but is dominated either by Douglas-fir (Fd) and/or western hemlock (Hw).

[2] EP384/85 consists of 12 PSPs located near Canal Flats, BC. These installations are composed of lodgepole pine (Pl) with scattered western larch.

PrognosisBC can use the FVS Fire and Fuel Extension model to generate standing dead tree information. For a planning study in Nelson Forest Region of BC, Greenough and others (1999) adjusted this extension based on fall information from a limited set of regional PSPs. The standing and fallen dead tree information was linked to a number of indicators to provide an environmental assessment. The Fire and Fuel Extension has not been parameterized for use in other areas.

Discussion

The integrated collection of dead and live trees on PSPs enables a tree to be followed through its entire development and breakdown. Knowledge of the source of death or timing of decay onset provides valuable information for understanding the breakdown of a dead tree. Likewise, the management of dead trees is tied to the management of live trees as a source of dead tree recruits. The integrated collection provides direct data ties for modelling the growth and yield of live and dead trees.

The measurement of standing dead trees in conjunction with live trees on GY PSPs is also more economical, as much of the measurement cost is associated with travel to the site. Furthermore, within the BC RIB GY PSP program we made a tradeoff between information and cost by measuring only standing dead trees greater than 10 cm DBH, while live trees are currently measured down to 2 cm DBH. The 10 cm limit reduces the variability of the number of dead trees per plot to measure and, therefore, the contractor uncertainty about the number of trees that will be measured.

The use of existing GY PSPs to obtain dead tree information is not without potential problems. As with any sampling, the user of the information must determine whether the information and any biases are appropriate. Biases may exist in plot placement. In BC, areas with forest health problems tended to be avoided when the PSP objective was assessment of potential tree growth. PSPs also tend to be located in areas with easier access (i.e., roads hopefully are not randomly located). Biases might also be caused by the physical act of measurement. In certain PSP programs in BC, at least until the mid-1970s, some sampling crews tended to push over standing dead trees to simplify plot establishment and measurement as dead trees were not considered important at the time.

The collection of dead tree information on PSPs must serve a use, whether it is a current need or a perceived future need. Managers must ensure that data are properly collected, stored, and summarized so that they are available to the users. The users must demonstrate to the managers that the data are serving a purpose and provide feedback to collection or data management needs. Furthermore, to ensure the success of a long-term information collection program, managers and users both must communicate the value of PSPs in the face of changing information needs to those who ultimately fund the program.

PSPs should be considered as one source for information on dead tree dynamics. PSPs may not be able to provide all needed information, some of which may have to be obtained by destructive methods. The small size of PSPs and their placement will most likely be inappropriate for investigating the role of standing dead trees in relation to organisms with larger space needs, and the appropriate linkages must be made through other knowledge and sampling tools. Additionally, information obtainable on PSPs might be obtained by other methods sooner (e.g., Huggard 1999). In BC, we still have a large need for basic dead tree information, and we need to use all the tools possible.

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Dead Wood and Fire Relationships in Southwestern Oregon Western Hemlock Forests[1]

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Abstract

The densities of large snags and down wood in western hemlock forests of southwestern Oregon are highly variable. Fire is a major disturbance process that contributes to the composition and structure of these complex forests. This study examines levels of dead wood by plant association, and relationships of dead wood with fire. Data were collected from 169 plots on the Rogue River, Siskiyou, and Umpqua National Forests in Oregon. Median snag densities ranged from 3 up to 18 snags/ha over the plant associations. Down wood medians ranged from 0 to 113 pieces/ha. Variation was high and there were no significant differences between plant associations within the Western Hemlock Series. Median fire return intervals ranged from 26 years to 85 years. Elevation, slope, and median fire return interval were the best predictors of dead wood density. The R-squared values improved when the warmest, driest plant associations were removed from the analyses. The high degree of variability in dead wood density and fire return intervals suggests that a single standard is not appropriate across southwestern Oregon. Landscape level prescriptions should incorporate extremes along with median values.

Introduction

Snags and down wood are important structure components of forest ecosystems (Harmon and others 1986). They play a role in microclimatic variation in the forest and provide habitat for a variety of life. Little data have been published on levels of dead material in southwestern Oregon.

The abundance of snags and down wood is determined by several factors. The initial density and size of a forest stand will regulate the potential for providing snags and down wood. Agents such as fire, wind, insects, and diseases kill trees often in episodic disturbances. The extent of this mortality depends on the severity and

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frequency of the disturbance. Fire and decay cause breakdown and consumption of snags and down wood.

Although all sizes of snags and down wood are important, recent emphasis by wildlife biologists has been on large diameter material. This material takes longer to grow and would take more time to replace if it were removed from a site.

Standards for large down wood and snags are found in the Northwest Forest Plan (Anonymous 1994). These standards are uniform across the complex climatic, edaphic, and vegetation conditions of southwestern Oregon. In this paper we analyze relevant data to examine variation and pattern of density of dead wood, and the relationship of dead wood with fire. Our objective is to provide a framework and understanding of processes for managers to make landscape level prescriptions for down wood and snags greater than 50 cm diameter.

Study Area

Data were collected from the Rogue River, Siskiyou, and Umpqua National Forests in areas that are characterized as Western Hemlock Plant Series (*Tsuga heterophylla* is the climax tree species). The Western Hemlock Series is partitioned into 14 plant associations, based on floristics and environment (Atzet and others 1996) *(table 1)*. The sites on the Siskiyou National Forest are in the mid-coastal sediments ecoregion, and sites on the Rogue River and Umpqua National Forests are in the southern Cascades and Umpqua Cascades ecoregions (Anonymous 1995). The climatic range is broad, from a mean annual temperature of 12 ˚C to 6 ˚C, and a mean annual precipitation of 292 cm to about 127 cm (Atzet and others 1996).

Table 1—*Plant associations, common names, and plant association codes in the Western Hemlock plant series in southwestern Oregon.*

Plant association	Common name	Code
Tsuga heteropylla-Abies concolor/ Acer circinatum-Berberis nervosa	Western hemlock-white fir/ vine maple-Oregon grape	TSHE-ABCO/ ACCI-BENE2
Tsuga heterophylla-Abies concolor/ Berberis nervosa	Western hemlock-white fir/ Oregon grape	TSHE-ABCO/ BENE2
Tsuga heterophylla-Castenopsis chrysophylla/Gaultheria shallon-Rhododendron macrophyllum	Western hemlock-golden chinkapin/salal-Pacific rhododendron	TSHE-CACH6/ GASH-RHMA3
Tsuga heterophylla-Pseudotsuga menziesii/Gaultheria shallon-SWO	Western hemlock-Douglas-fir/Salal-SWO	TSHE-PSME/ GASH-SWO
Tsuga heterophylla-Thuja plicata Rhododendron macrophyllum /	Western hemlock-Western red cedar/Pacific rhododendron	TSHE-THPL/ RHMA3
Tsuga heterophylla/Acer circinatum/Gaultheria shallon-SWO	Western hemlock/Vine maple/Salal-SWO	TSHE/ACCI-GASH-SWO
Tsuga heterophylla/Acer circinatum-Rhododendron macrophyllum	Western hemlock/Vine maple-Pacific rhododendron	TSHE/ACCI-RHMA3
Tsuga heterophylla/Gaultheria shallon-Berberis nervosa-SWO	Western hemlock/Salal- Oregon grape-SWO	TSHE/GASH-BENE2-SWO

Tsuga heterophylla/Gaultheria shallon-Rhododendron macrophyllum-SWO	Western hemlock/Salal- Pacific rhododendron-SWO	TSHE/GASH-RHMA3-SWO
Tsuga heterophylla/Gaultheria shallon/Polystichum munitum-SWO	Western hemlock/Salal/ Western swordfern-SWO	TSHE/GASH/ POMU-SWO
Tsuga heterophylla/Polystichum munitum-SWO	Western hemlock/Western swordfern-SWO	TSHE/POMU-SWO
Tsuga heterophylla/ Rhododendron macrophyllum- Berberis nervosa-SWO	Western hemlock/Pacific rhododendron-Oregongrape-SWO	TSHE/RHMA3 - BENE2-SWO
Tsuga heterophylla/ Rhododendron macrophyllum- Gaultheria shallon-SWO	Western hemlock/Pacific rhododendron-Salal-SWO	TSHE/RHMA3 - GASH-SWO
Tsuga heterophylla/Vaccinum ovatum/Polystichum munitun	Western hemlock/Evergreen huckleberry/Western swordfern	TSHE/VAOV2/ POMU

Soils are of sedimentary and volcanic origin. Soils on the Siskiyou National Forest sites are most commonly derived from sandstones, while sites from the Cascade Mountains of the Rogue River and Umpqua National Forests are commonly derived from andesites and basalts. Other parent materials are present, but at lower proportions.

Field Data Collection

Data were collected from permanent plots that were located on the Rogue River, Siskiyou, and Umpqua National Forests. Plots were located so that the variation in vegetation over the landscape was represented. Within plots, a single plant association was present. The full range of elevation, aspect, slope, and rock types were sampled. Plots were selected to minimize previous human disturbance, and tended toward fully stocked, mature stands.

Five subplots were established around each plot using the USDA Forest Service's Pacific Northwest Region 10-point timber inventory diamond cluster protocol (Anonymous 1970). Within each variable radius subplot, the diameters of all species of trees and snags were recorded. The heights and ages of five site trees of each dominant species and three to five site trees of each codominant species were recorded. The ages were estimated as number of annual rings at dbh when the core reached the pith. Where the cores did not reach the pith, age was estimated by extrapolation using the diameter and rings per inch closest to the inner end of the core. Height, diameter, species and decay class (Cline and others 1980) were recorded for each snag.

The topographic variables of elevation, aspect, percent slope, and microposition were recorded for each plot. Microposition was defined as ridge top, upper one-third of slope, middle one-third of slope, lower one-third of slope, bench, toe of slope, canyon bottom, edge or in wetland basin, and draw or intermittent stream bottom.

Down wood data were collected along three, 21-meter transects with random-direction segments. At the point of intersection with a discernible piece of wood at least 12.5 cm in diameter, we recorded the diameter at the intersect, large end and small end diameters, length, species, and decay class were recorded. Decay was recorded as classes 1 to 5 (Fogel and others 1972).

Analyses

Analyses were conducted at the landscape scale and show the relationship of snags and down wood by plant association.

Densities of live trees, snags, and down wood exhibit a distribution that is skewed to the right. Measures of central tendency were expressed as Weibull medians and quartiles, which account for this skewedness, compared with medians from normal distributions, which simply describe the middle value of the distribution. The Kruskall-Wallace H-test was used to test differences between plant associations. Linear and nonlinear regression were used to show relationships between dead wood density and environmental variables and disturbance variables. The SPSS software[5] (Anonymous 1998) was used for all analyses.

The disturbances were derived by first listing, by species, the aged trees within each plot in descending order of age. Patterns of age and/or species change were noted. When a pioneer species (Douglas-fir, ponderosa pine, Shasta red fir) was present, the age was noted. If one or more trees of a pioneer species in a discernible age class (approximately a 30 year period) were present, that was assumed to be the result of a disturbance event. A surety rating for each disturbance event was assigned based on the tree age estimate, whether more than one tree was present in the age cohort (with multiple trees indicating higher surety), and the species of trees present. The rating ranged from 1 (unsure) to 10 (positive) and only events with a rating of 8 or higher was used in this analysis. A fire severity rating was also assigned: 1 = low severity—climax trees established after the disturbance; 2 = moderate severity—pioneer species established after the disturbance, but with older climax species that survived the event; and 3 = high severity—pioneer species established after the disturbance with climax species coming in later. These are patterned after Brown's (1994) fire regime severity classes. Date of disturbance was calculated using tree ages and plot data. Disturbance dates derived from tree age and stand structure data, rather than fire scar data, is a more liberal approach. It will likely detect disturbances not usually shown by fire scars. This technique has been used by others (Agee 1991, Arno and others 1997). It may be possible that disturbances other than fire were detected. Our data show that fire was overwhelmingly the dominant disturbance in this plant series; hence, the probability of a fire disturbance is quite high. Only disturbances before 1930 were used in the analyses because we believe fire regimes could have been altered by substantial European influence after that time.

Density of down wood was calculated using the methods described by De Vries (1973). Total dead wood was calculated as the sum of snags and down wood.

Results and Discussion

The live tree community forms the pool from which snags are derived. The median density of large live trees range from about 67 to over 134 trees per hectare and provide an abundance of potential dead wood *(table 2)*. The median number of

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[5] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

snags ranges from about 3 up to about 18 per hectare, although there are no significant differences between plant associations. The quartile range of snags shows that snags were absent on several of the plant association plots and that a high degree of variability is associated with these data. Abundance of down wood reflects the same pattern. Large down wood was absent on plots in half of the plant associations. The variation was quite high: for example, in the TSHE-CACH6/GASH-RHMA3 Plant Association, the quartile range was zero to 132 pieces per hectare *(table 2)*.

Table 2—*Comparison of live tree, snag, and down wood (50 cm+ diameter) density per hectare in Western Hemlock Plant Associations in southwestern Oregon.*

Plant association	N[1]	Median and quartile range of trees or pieces per hectare[2]		
		Live trees	Snags	Down wood
TSHE-ABCO/ACCI BENE2	13	93.5 (66.3-118.4)	10.0 (0-13.8)	25.9 (8.2-95.1)
TSHE-ABCO/BENE2	11	100.5 (66.9-147.7)	3.6 (0-19.2)	30.9 (0-52.4)
TSHE-CACH6/ GASH-RHMA3	6	88.1 (68.3-117.2)	12.2 (7.1-20.6)	13.3 (0-132.2)
TSHE-PSME/GASH-SWO	5	72.9 (27.7-105.8)	8.1 (2.2-20.9)	17.8 (0-60.8)
TSHE-THPL/RHMA3	6	98.4 (81.3-138.0)	16.2 (0-31.8)	18.5 (0-101.3)
TSHE/ACCI-GASH-SWO	10	69.0 (51.5-81.2)	9.6 (0.8-14.8)	91.2 (10.9-147.3)
TSHE/ACCI-RHMA3	29	134.7 (99.1-156.4)	12.2 (3.8-18.9)	16.1 (0-92.7)
TSHE/GASH-BENE2-SWO	17	77.2 (67.5-123.2)	12.3 (7.8-20.8)	32.1 (10.9-118.9)
TSHE/GASH-RHMA3-SWO	20	94.9 (79.3-122.2)	11.0 (3.1-19.9)	24.7 (0-84.8)
TSHE/GASH/POMU-SWO	14	77.5 (63.2-88.6)	13.8 (8.3-30.6)	113.4 (22.7-175.7)
TSHE/POMU-SWO	7	79.7 (72.1-97.9)	13.3 (8.3-30.1)	59.6 (26.9-107.2)
TSHE/RHMA3-BENE2-SWO	5	114.5 (74.1-139.5)	13.2 (7.3-24.5)	3.7 (0-52.1)
TSHE/RHMA3-GASH-SWO	14	103.9 (93.3-166.4)	18.0 (6.3-27.3)	0 (0-13.8)
TSHE/VAOV2/POMU	12	67.3 (50.1-155.3)	12.3 (6.8-20.1)	58.1 (6.7-190.5)

[1] Number of plots.

[2] Median values of live trees per acre are significantly different between plant associations ($P<0.001$; Kruskal-Wallis H-test), median values of snags per acre are not significantly different between plant associations ($P=0.42$, Kruskal-Wallis H-test), and density of down wood is not different between plant associations ($P=0.52$; Kruskal-Wallis H-test).

Disturbance intervals were recorded from about 900 ybp to about 60 ybp. Median fire return intervals for plant associations range from a low of 26 years for the TSHE/RHMA3-BENE2 plant association, to a high of 85 years for the TSHE/VAOV2/POMU association *(table 3)*, The confidence intervals are wide, reflecting a high degree of variability.

Table 3—*Weibull medians and confidence intervals for the plant associations in the Western Hemlock Series.*

Plant association	Weibull median (years)	80 percent CI
TSHE/RHMA-BENE2	26	12-165
TSHE-PSME/GASH-SWO	34	15-164
TSHE-CACH6/GASH-RHMA3	43	19-147
TSHE/ACCI-GASH-SWO	43	14-151
TSHE/ACCI-RHMA3	48	15-145
TSHE-ABCO/BENE2	53	17-156
TSHE-ABCO/ACCI-BENE2	59	21-192
TSHE/RHMA3-GASH-SWO	61	14-265
TSHE/GASH-BENE2-SWO	67	20-188
TSHE-THPL/RHMA3	67	20-251
TSHE/POMU-SWO	69	33-297
TSHE/GASH-RHMA3-SWO	81	26-190
TSHE/GASH/POMU-SWO	81	26-275
TSHE/VAOV2/POMU	85	30-243

Snags or down wood alone showed poor correlations with fire and environmental variables when compared with total dead wood density.

Percent slope explained 68 percent of the variation in total dead wood *(table 4)*. The highest densities of dead wood occurred on the gentlest slopes and the lowest on slopes over 50 percent. Elevation explained 41 percent of the variation in total dead wood density. The highest amounts were at elevations less than 689 m and densities decreased as the elevation increased. Sites on gentle slopes and lower elevations often correspond to riparian areas in the Western Hemlock Series and are areas where fires are often less severe. Aspect explained a little over 28 percent of the variation, though the equation was not significant, and microposition explained virtually none of the variation in total dead wood density *(table 4)*. Because elevation and slope are highly correlated in our data, it is not appropriate to use them together in a multiple regression.

Table 4—*Regression analyses of environmental variables and total dead wood densities.*

	RSQ	df	sigf	b0	b1	b2
Total dead wood						
Elevation	0.410	11	0.055	78.90	-0.026	2.9E-06
Slope	0.680	11	0.002	-19.27	1.264	0.0006
Microposition	0.063	11	0.699			
Median aspect	0.283	11	0.160	19.15	0.028	0.0001

The variables mean fire severity, severity of the last fire, and length of the last fire interval were all highly correlated, and as such, were not appropriate for use together in multiple regression. When density of snags and density of down wood were combined into a total dead wood pool, regression showed that the length of the last fire interval explained over 27 percent of the variation (R-squared = 0.274), and fire severity explained slightly less *(table 5)*. Median fire return interval (FRI) explained over 42 percent of the variation with a quadratic function. In all cases except median FRI, nonlinear regression did not improve the fit of the data. The large amount of variation made it difficult to detect a difference between linear and nonlinear relationships. Fire severity was negatively related to total dead wood, and length of the last fire interval was positively related.

Table 5—*Regression analyses of mean fire severity, last fire severity, last fire interval length, and Weibull median fire return interval as predictors of total dead wood densities. Equations are shown for all data, and data with two outliers removed.*

	R-SQ	df	sigf	b0	b1	b2
Total dead						
Mean fire severity	0.221	12	0.090	111.43	-40.99	
Last fire severity	0.201	12	0.108	51.68	-19.93	
Last fire interval	0.274	12	0.055	1.75	0.22	
Median FRI	0.422	11	0.049	33.96	- 0.76	0.011
Total dead–no outliers						
Mean fire severity	0.637	9	0.010	406.27	-323.83	66.31
Last fire severity	0.609	9	0.015	97.56	- 86.01	20.92
Last fire interval	0.422	9	0.085	12.56	- 0.12	0.002

Interestingly, when the two outliers with the highest total dead wood values are removed from the data set, and nonlinear analyses are used, the R-squared values increase dramatically. Mean fire severity has an R-squared value of 0.637 (p=0.01), and length of time between the last two fires has an R-squared of 0.422 (p=0.085). These two outlier data points represent the warmest, driest plant associations, which may follow a different pattern than the warm, moist western hemlock areas.

Multiple regression with elevation and median FRI was highly significant in explaining the densities of dead wood, where density = -27.023 + 0.245 (median FRI) + 1.116 (slope). (R-squared = 0.76).

Overall, the length of the last fire interval is positively correlated with total dead wood. This suggests that for 50 cm+ dead material, fire suppression has likely caused an increase in material, and plant associations with longer fire return intervals are capable of carrying more dead wood. Average fire severity and severity of the last event are negatively correlated with total dead material; that is, the more severe the event, the less 50 cm+ material remains. This may seem counter-intuitive, because high severity fires generally correspond to stand replacement fire, which may yield high levels of dead wood. In southwestern Oregon, in the mature stands we sampled, multiple intervening low intensity fires likely consumed a great deal of the dead wood generated by stand-replacing events. The median FRI data show an inflection point around 50 years, after which the amount of dead wood increases sharply.

Our data show levels of snags and down wood are highly variable over the landscape. This variability should be retained, and stratification by plant association will aid prescriptions. Some portion of the landscape will have little or no dead wood, while other portions will have a great deal. The distribution should be based on an integration of desired conditions. For example, fire and wildlife managers may suggest leaving most in riparian areas, a prescription that is supported by the data on elevation and percent slope. If the management objective is to remove dead material, leave some part of the landscape with the extremes and remove wood from areas with median amounts.

Fire return intervals in Western Hemlock Plant Associations in southwestern Oregon are shorter than those further north. They are variable, as are the severities. This chaotic nature of fire across the landscape is the primary means of creating diversity in composition and structure for which the southwestern Oregon forests are known. Fire should be returned to the forest with landscape level planning and allowed to burn in non-uniform, chaotic patterns.

Our data indicate, the higher the severity the fire, the less large material will remain. Attempting to retain too much coarse wood will have an effect similar to fire control. Over the long run, the proportion of high intensity fire will increase. Consequently, the potential for soil damage and reduction of late seral conditions will increase. This "boom-and-bust" cycle is more characteristic of the temperate forests to the north. It may have negative effects on local species that evolved with frequent, but low intensity fire.

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The Number and Composition of Snags in the Pine-Spruce Stands of the Bialowieza National Park, Poland[1]

Wieslaw Walankiewicz[2]

Abstract

This paper documents data on standing dead trees (snags) in the pine-spruce (Norway spruce *Picea abies,* Scots pine *Pinus sylvestris*) natural stand in Bialowieza National Park (BNP) in northeast Poland. Trophically, this mostly coniferous stand represents one of the poorest habitats of the BNP, and this stand has never been cut. There are few tree species of significance, i.e., Scots pine, Norway spruce, hornbeam *Carpinus betulus* and two birch species *Betula verrucosa*, *B. pubescens*. Other tree species are scarce. Altogether 6.25 ha were measured within 25 samples. Among tree species, the proportion of dead standing trees was 0-58 percent of the total basal area and 0.9-59 percent of total density. The tree species dominance pattern shows a different pattern of change. Pine is declining, while hornbeam is invading the stand from bordering deciduous stands and now is a well regenerating tree species. Spruce regeneration slowed within the last 20 years. Until about 10 years ago, birches were not regenerating and were declining from the plot. Recently, within no more than the last 10 years, birches are regenerating within the plot again. All these changes reflect snag characteristics and composition.

Introduction

Most of the lowland forests of the European temperate zone underwent severe anthropogenic transformations before modern research started. However, the forests of the Bialowieza National Park are an exception. The Bialowieza Forest complex (total area 1,500 km^2) is situated on the Polish-Belarussian border *(fig. 1).* Its western part (c. 600 km^2) belongs to Poland. This forest is a remnant of the vast lowland forest that once covered central parts of Europe. The majority of stands in the Polish part of the forest are now under management, but 47.5 km^2 of the best preserved primeval stands has been protected within the Strict Reserve of the Bialowieza National Park (SR BNP) (Falinski 1986, Tomialojc 1991). This part has never been cut because it was protected as hunting grounds for the Polish kings and later the Russian czars since the early 15th century. After World War I it became the first Polish national park. Human presence is very restricted to some tourist trails only.

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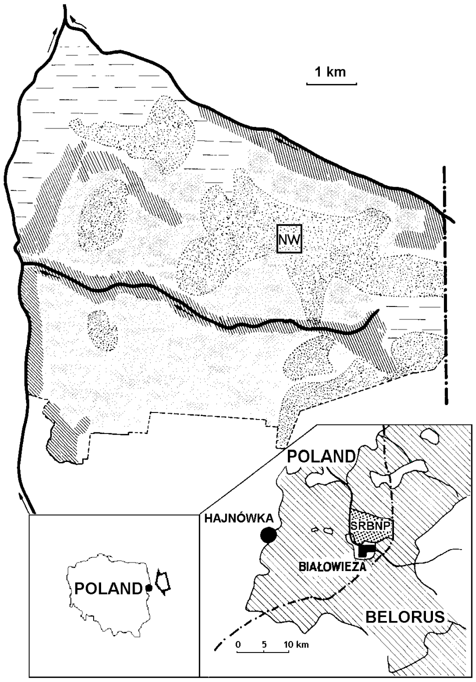


Figure 1_A map of the Polish part of the Bialowieza Forest showing the location of the strict reserve (SRBNP) and study plot (NW).

The old-growth preserved in SR BNP are mainly the linden-hornbeam *Tilio-Carpinetum* type (44.4 percent), swampy deciduous (26.6 percent), and dry coniferous (28.1 percent) stands. The old-growth stands of SR BNP are multi-storey, mixed-species, uneven-aged, composed of trees reaching exceptional height, and contain large amount of dead standing trees (snags) and uprooted trees. In spite of the fact that many authors stressed the high amount and the importance of the dead wood in this forest, the quantitive data are scarce and only general (Falinski and Herezniak 1977, Kirby and others 1991, Piotrowski and Wolk 1975). Although most of the SR BNP is covered by deciduous woodland, the coniferous stands (i.e., pine-spruce stands [Norway spruce *Picea abies,* Scots pine *Pinus sylvestris*]) contribute greatly to sustaining biological richness of BNP. For instance, several bird species are recorded mostly or exclusively in this conferous habitat (Tomialojc and others 1984).

Structure and dynamics of the BNP natural stands have been studied for almost 80 years (Falinski 1986, Paczoski 1925). Both deciduous and coniferous stands of SR BNP are not in a state of climax. In the linden-hornbeam *Tilio-Carpinetum* type, the spruce has decreased steadily in number (Falinski 1986). In coniferous forests, i.e. pine-spruce type, the pine share has decreased as well. Comparing tree distribution maps from 1903 and 1958, Czerwinski (1968) stated that during the investigated period, pine decreased substantially and it was replaced by the spruce and oak *Quercus robur*. Wloczewski (1972) and Kowalski (1972) also noticed directional change of the pine stands into the spruce stands. Even more, an increase of the hornbeam *Carpinus betulus* in number in coniferous stands has been noticed (Gunia 1972; Kowalski 1972, 1982).

This study aims to describe the occurrence and characteristics of the snags (i.e., dead standing trees) within the pine-spruce stands of the SR BNP under the dynamic process ongoing in this stand with time. Snag characteristics have never been described in details in these forests, and only Jakubowska-Gabara and others (1991) have assessed how many dead standing trees were among all trees in the same type of stand of BNP.

Study Plot

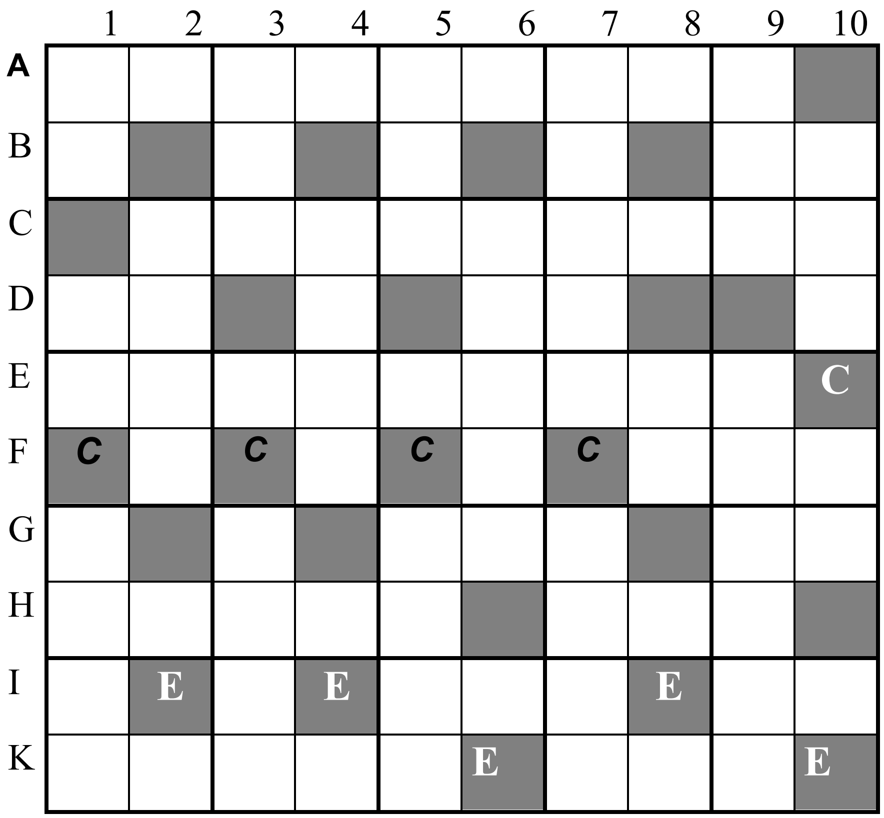
The NW 25-ha study plot (500 m x 500 m, located in compartment 318A; Tomialojc and others 1984) was chosen. It is covered by the pine-spruce natural stand, which has never been cut. The association of this kind usually develops on sandy soils in upper parts of the BNP. Trophically, it represents one of the poorest habitats in SR BNP. The main canopy is formed of pines, while the lower one is composed of spruces with few pines, birches *(Betula verrucosa, B. pubescens),* and oak. In the plot, spruce dominates numerically over pine. The young tree-layer is composed mostly of hornbeams and spruces. The herb layer is sparse, composed of *Oxallis acetosella* and *Vaccinium myrtillus*. Forest openings are dominated by *Calamagrostis arundinacea* and *Pteridium aquilinum*.

The plot has been subdivided into a 50-m grid. That area has been under ornithological investigation since 1975 (Tomialojc and others 1984). Since that time an increase of hornbeam in number is very visible. The young generation of *Carpinus betulus* invades the area from the north and especially from the south, i.e., from the transition border zones with the deciduous stands. This transition, where coniferous stands turn gradually into deciduous stands, is 50-80 m wide. Matuszkiewicz and Matuszkiewicz (1954) mapped the whole study plot as the pine forest *Pinetum Myrtylli* association.

Methods

In June and July 1998 I counted and measured the diameter at breast height (dbh) of all trees that reached at least 1.5 m tall within the 50 m x 50 m squares (samples). One such square (0.25 ha each) was chosen randomly within every ha of the study plot *(fig. 2).* Altogether 6.25 ha were measured within 25 square samples. Both live and dead trees were identified to species. The recognition of dead trees caused no serious problems, since there were only two coniferous and a few deciduous species. The exception is the two birch species, which I treat jointly since they were uncommon and I was unable to distinguish snags of those species.

Additionally, to illustrate the hornbeam invasion in the northwest plot, I compared the diameter distribution within the central part of the plot with that of the ecotonal (southern) part of the plot. For this, five samples were chosen in both parts *(fig. 2).*



	1	2	3	4	5	6	7	8	9	10
A										▨
B		▨		▨		▨		▨		
C	▨									
D			▨		▨			▨	▨	
E										▨ C
F	▨ C		▨ C		▨ C		▨ C			
G		▨		▨				▨		
H						▨				▨
I		▨ E		▨ E				▨ E		
K						▨ E				▨ E

500 x 500 m = 25 ha

Figure 2_Distribution of measured squares within the study plot (E = ecotone, C = center).

Results and Discussion

Snag Density by Diameter Class

Among live trees, spruce and hornbeam together comprise 86 percent of the stand by number of trees. Pine (9 percent) is the third most abundant species *(fig. 3)*. Snag species composition is utterly different. Spruce and pine snags comprise 88 percent of all dead trees *(fig. 4)*. When considering only trees with diameter ≥ 10 cm, the share of spruce snags and pine snags altogether increased to 92 percent *(fig. 5)*. Together with birch, these three species compose 98 percent of all such defined snags. The very small share of the hornbeam among snags is easy to explain when I compare the dbh class distribution of pine, spruce, and birch with dbh distribution of the hornbeam *(figs. 6-9)*. The hornbeam is represented almost exclusively by trees with dbh not bigger than 20 cm *(fig. 8)*.

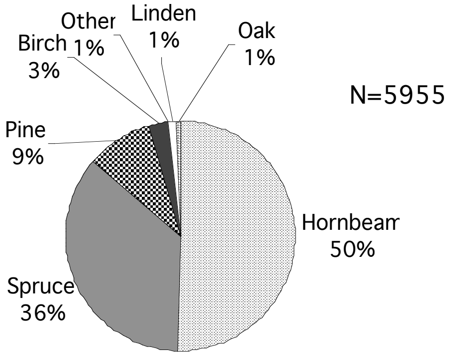


Figure 3_Share of different species in the living tree community.

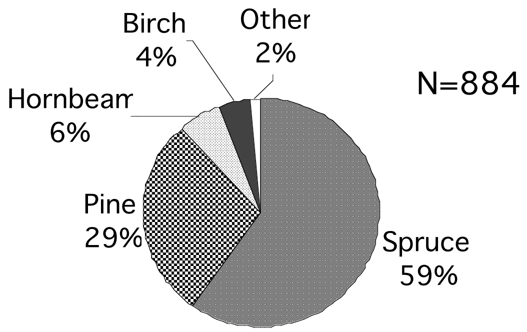


Figure 4_Share of different dead tree species among the snags within the study plot.

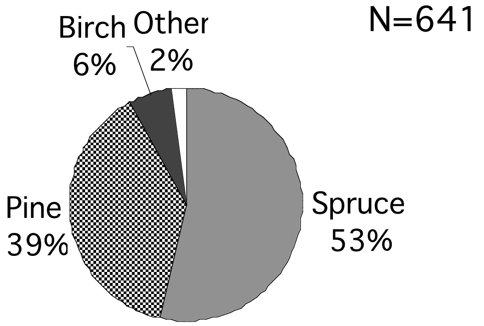


Figure 5_Share of different dead tree species with the ≥ 10 cm diameter classes.

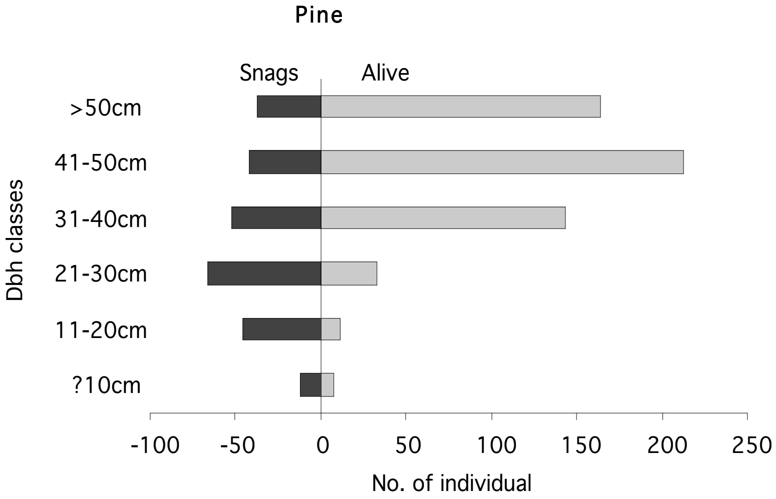


Figure 6_Structure of the pine tree stand according to diameter classes (dbh).

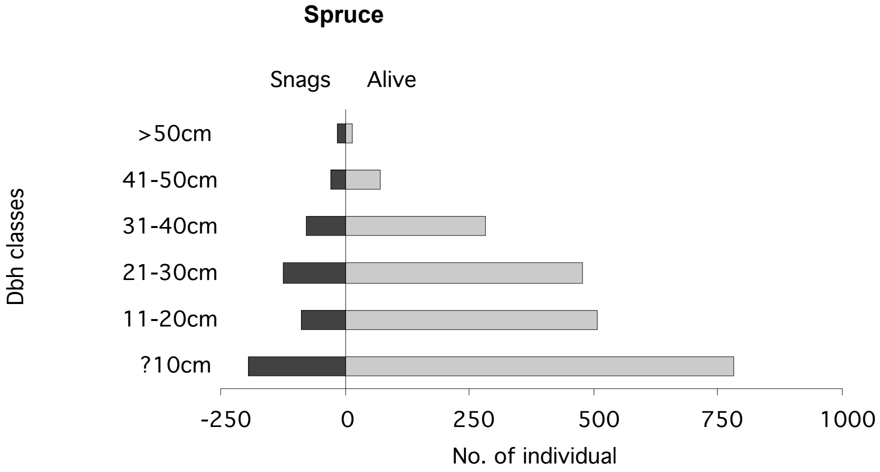


Figure 7_Structure of the spruce tree stand according to diameter classes (dbh).

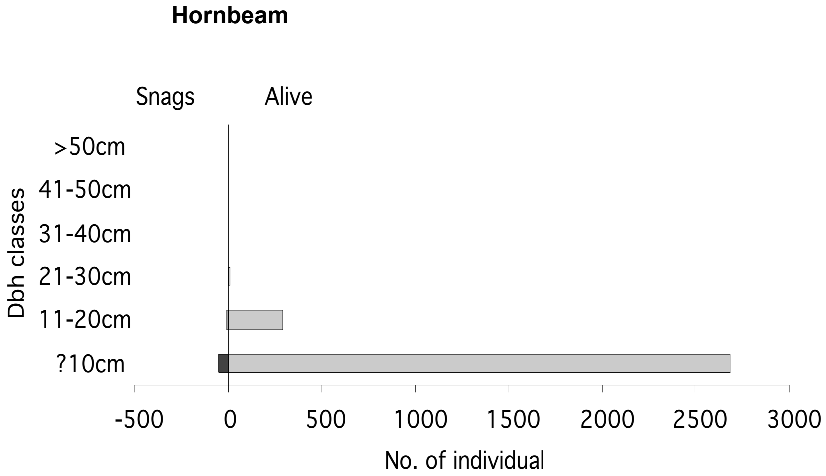


Figure 8_Structure of the hornbeam tree stand according to diameter classes (dbh).

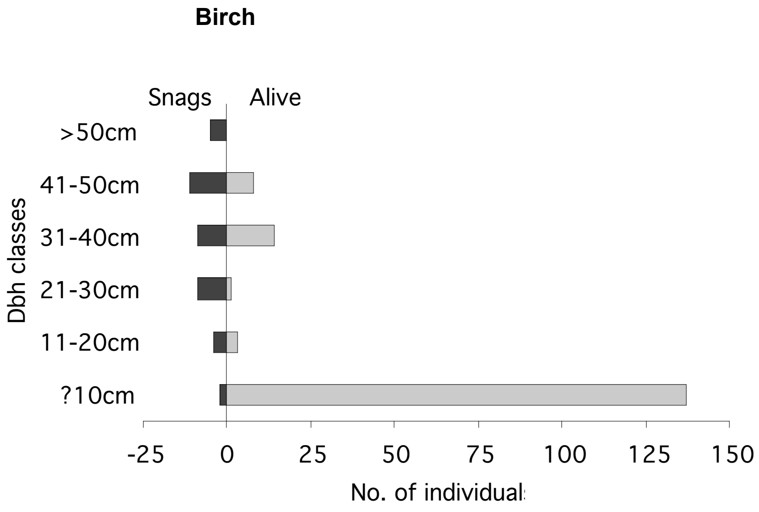


Figure 9_Structure of the birch tree stand according to diameter classes (dbh).

Total snag density concerning only trees with ≥ 10 cm dbh is 102.6/1ha. The spruce and the pine snags are the most numerous, reaching density 54.9/ha and 39.5/ha, respectively. Birch snags occur in much lower density (5.8/ha). High density of the spruce snags is a result of bark beetle *(Ips typographus)* outbreak in BNP during 1994-1996 years. Jakubowska-Gabara and others (1991) reported from 1990 (i.e., data collected before bark beetle outbreak appeared) that the same forest type in SR BNP had about three times lower spruce snag density. They also found that the pine snags were denser, exceeding 50 snags/1ha.

What Proportion of Standing Trees are Dead?

Pine and spruce compose 91.0 percent of the total basal snag area and 93.1 percent of standing dead trees. Total basal area of dead standing trees is relatively high compare to other measured stands (Tritton and Siccama 1990). The pine and spruce proportion of dead standing trees of the total basal area was similar *(table 1)*. Birches, which are uncommon, have high proportion of dead trees expressed either as basal area or percent of stand.

Table 1_*Basal area and density of living and dead steams ≥ 10 cm dbh, and standing dead trees as a percent of stand total.*

Species	Living	Dead m^2 ha^{-1}	Pct dead	Living	Dead stems ha^{-1}	Pct dead
Scots pine	15.5	4.2	21.3	89	40	31.0
Norway spruce	12.1	3.9	24.4	224	55	19.7
Hornbeam	0.9	0.0	0.0	56	0	0.0
Birch	0.5	0.7	58.3	4	6	60.0
Other	0.9	0.1	10.0	11	1	8.3
Total	29.9	8.9	23.1	384	102	21.0

Diameter of Snags (Dbh)

The diameter of the two birch species and pine (birch x = 37.1 cm, S.D. = 12.7, n = 38, pine x = 34.0 cm, S.D. = 14.5 n = 247) are greater than that of spruce (x = 27.8 cm, S.D. = 11.5, n = 343). This is because the pine and birch snags originated mostly from older trees *(figs. 6, 9)*. Spruce snags have thinner dbh because they originated mostly from trees of lower dbh classes, including young trees that died due to a self-thinning process *(fig. 7)*. The composition and characteristic of snags are affected by such processes as retreat (pine) and regeneration and competition (spruce, birch and hornbeam).

Regeneration of Different Tree Species

Within the smallest dbh class, 2,591 hornbeams, 649 spruces, 135 birches, and 8 pines were found. This suggests ongoing intense change in the composition of the stands that were analyzed.

According to Falinski (1986), the spruce regenerates fairly well in coniferous forests on dry hills of the BNP. The spruce diameter distribution, especially the high number of trees in the smaller diameter classes (1-2), indicates good regeneration of this species *(fig. 7)*. It is also the most numerous among tree species in the middle diameter classes (750 spruces versus 176 pines in diameter 21-40 cm). This species will likely remain an important component of the analyzed stand for many years.

The large number of pines in the larger (4-6) diameter classes and few in the lower classes (1-3) indicates that this species has ceased to regenerate and is retreating from the stand *(fig. 6)*. In the first diameter class only eight pine trees were found. The retreat of the pine from BNP has been well documented (Czerwinski 1968, Gunia 1972, Kowalski 1972, Matuszkiewicz 1952, Paczoski 1930, Wloczewski 1972). Some old pines occur in linden-hornbeam stands farther than 1 km from the conifer part of the forest (Walankiewicz, pers. observ.), suggesting that in the past the pine had much wider distribution than at present and that the area covered by pine has decreased. Korczyk (1994) found that this species lives up to 400 years in the Bialowieza Forest.

Although hornbeam is the most numerous tree species, it occurs almost only in the first and second dbh classes *(fig. 8)* (an average dbh of all hornbeams equals 4.0 cm, S.D. ± 4.17, n = 3,984 and 41 percent of all living hornbeams have dbh □ 2cm). Because it grows in SR BNP up to a diameter of 100 cm (Falinski 1977), this means that occurrence of this species within the plot is a new phenomenon. I have visited this plot several times a year from 1975 to 1998 conducting ornithological research (Tomialojc and others 1984). During that period, in the northwest plot, I observed a continuous increase of young hornbeams in number. The first hornbeam dbh class is three times more numerous than the same class of the spruce *(figs. 7, 8)*. Furthermore, 25 years ago many hornbeams in the study plot were shaped like trees that suffer poor growth conditions (i.e., poor soil). Currently, hornbeams look different, and they are shaped like young fast growing trees. Apparently this species is a very new invader in this stand. It is visibly more numerous in both the southern and northern parts of the plot, which border linden-oak-hornbeam stands, than it is in central part. Furthermore, within the study plot, there are few if any hornbeams old enough to produce seeds. As a matter of fact, well regenerating hornbeam originated mostly, if not only, from trees that are outside the study plot. Gunia (1972) and Kowalski (1972, 1982) noticed an increase in the number of hornbeam in coniferous stands of the BNP, but they did not expect the fast transformation described in this work.

The birches are represented mostly in the youngest class. Older/mature birches were low in the plot *(fig. 9)*. Only 22 birches within classes 2-6 were found within the 6.25 ha studied. In the 2-6 dbh classes there are more dead (62.1 percent) than live (37.9 percent) birch trees. This shows that until 10 years ago birches were not regenerating and retreating from the plot. Every year since 1975, I conducted ornithological observations in the northwest plot and observed within no more than the last 10 years that the birches started to regenerate within this plot again *(fig. 9)*. It happened in gaps where spruces were knocked down by wind. Birches are very rare in neighboring linden-hornbeam stands as well.

Directional Changes in Tree Stand Composition

Each tree species within the study plot are showing a different pattern of change. Pine density is declining while spruce, hornbeam and birches all seem to be well-regenerating tree species. However, because young birches are 5-20 times less numerous than hornbeam and spruce, the two latter species are most important for the future of the stand. But is the proportion of spruce-hornbeam stable within the studied plot?

To answer this question I compared separately the stand diameter structure of both species the the central and ecotonal (southern) parts of the plot. Such comparisons reveal that hornbeam regenerates in ecotonal part very well, but the spruce regeneration there is poor *(fig. 10)*. Clearly in this part of the study plot, the smallest spruce dbh classes are less numerous than the middle diameter classes of this tree species. Within the first dbh class, 1,651 hornbeams were found and only 20 spruces *(figs. 10, 11)*. This suggests that spruce regeneration slowed down there within the last 20 or so years. It is very likely that hornbeam will soon overtake this part of the stand reducing substantially the proportion of spruce. In 1975, young spruces 1-1.5 m tall were common in this northwest plot (Tomialojc and others 1984; Walankiewicz, pers. observ.). In the central part of the plot, however, the number of spruce and hornbeam in the first dbh class are similar (96 spruces vs. 94 hornbeams; *figs. 10, 11)*. This means that in the future this part of the stand will be covered by mixed spruce-hornbeam forest with a mixture of some old pine.

Summing up, there are five visible processes/changes ongoing in the tree stand within the study plot:

- Decrease of the pine in density; this species does not regenerate.
- Spruce, which dominates numerically over pine, regenerates well in the central part of the plot.
- In the ecotone, close to deciduous stands, the spruce regeneration is hampered by invasive young hornbeams.
- Hornbeams invade the plot from bordering deciduous stands and regenerate very well between older spruces and pines.
- Birches, which were close to extirpation, show renewed regeneration within the study plot.

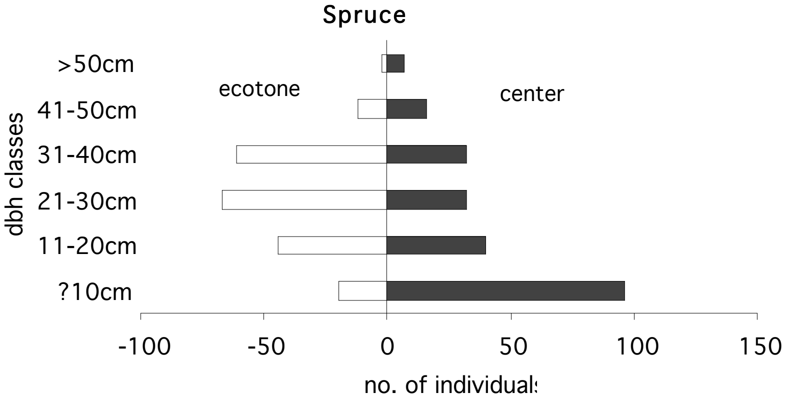


Figure 10_The structure of the spruce stand (live trees) in diameter classes within the central and ecotonal parts of the NW study plot.

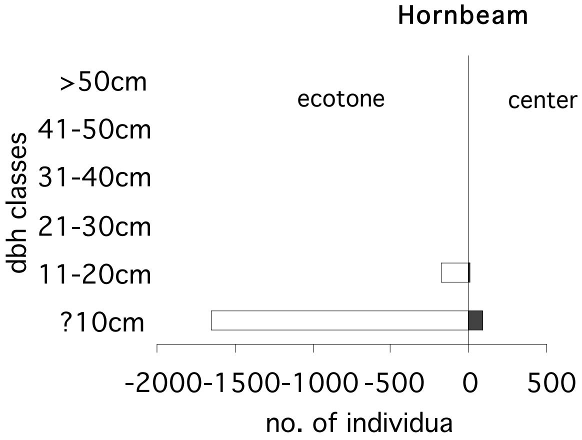


Figure 11_The structure of the hornbeam stand (live trees) in diameter classes within central and ecotonal parts of the NW study plot.

Durability of Snags and Ratio of Different Tree Species as Snags

Most of the snags (98 percent) are composed of spruce, pine, and birch. All of them are represented among live trees less numerously than among dead ones *(figs. 3, 5).* This is the result of the numerous occurrence of the hornbeam, which is too young to produce snags.

The ratio of different snag species tells us nothing about mortality of the different tree species. The relatively high share of pine among dead standing trees—39 percent among dead and only 9 percent among alive *(figs. 3, 5)*—does not mean high mortality of this species. Rather, it reflects high durability of pine snags. Many pine trees within northwest plot were dead in 1975 when the plot was marked—after 25 years they remain standing. One well-known pine snag has been standing next to the tourist path more than 50 years. Spruce's high share of snags, among other dried trees, actually reflects the high mortality of this species that was caused by the bark beetle outbreak in 1994-1996. In May 2000, many spruce snags within the plot are fell after the previous winter. Spruce snags apparently stand only for a few years after the tree is dead.

Assuming that the observed tendencies of the tree stand development will last, I predict the following changes in the snag composition within the studied stand:

- Within 2-3 years, the number of spruce snags will decrease by about two-thirds. The spruce snags will fall down due to the rotting processes in lower part of trunk.
- Birch snags, which are much less numerous than other species, will gradually disappear from the stand.
- The number of pine snags will remain rather stable for many years because of their high durability.
- It will take another 20 or more years before the first hornbeam snags of diameter 20-30 cm appear in the stand.

Some processes within the study plot were recorded in other parts of the SR BNP, especially a decrease of the spruce and an increase of linden in deciduous stands. This change was explained as a return of the forest to its natural state after extensive disturbance from excessive game foraging (Falinski 1986), as a directional change caused by changing climate (Bernadzki and others 1991, Kowalski 1882), or as a result of marshland drainage in the Belarussian part of the BNP (Bucholz 1968). All those factors seem to be additive, not compensatory.

Acknowledgments

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Demographics and Dynamics in the Cascades Forests

A Coarse Wood Dynamics Model for the Western Cascades[1]

Kim Mellen[2] and Alan Ager[3]

Abstract

The Coarse Wood Dynamics Model (CWDM) analyzes the dynamics (fall, fragmentation, and decomposition) of Douglas-fir *(Pseudotsuga menziesii)* and western hemlock *(Tsuga heterophylla)* snags and down logs in forested ecosystems of the western Cascades of Oregon and Washington. The model predicts snag fall, height loss and decay, and log decay at 5-year intervals for a period of 300 years. Snags either fall whole or in parts, creating down logs. Snags also decay from a hard to soft condition. Logs decay more slowly than snags, from sound to decayed conditions, and eventually disappear into the forest floor as duff. Snag fall and height loss rates were derived from Forest Inventory and Analysis (FIA) remeasurement data on private lands in western Washington. Decay rates were obtained from various studies conducted in the western Cascades of Oregon and Washington. The model can track remnant snags and logs (i.e., those existing on site at the beginning of the assessment time) and new snags and logs created from green trees.

Introduction

Managers of forested lands in the Pacific Northwest are required to manage for snags and logs, or coarse woody debris (CWD), in timber harvest units. Coarse woody debris is a highly dynamic ecosystem component, as snags fall over time and both snags and logs decay. Therefore, managing for these habitat components through time requires knowledge of the dynamics of CWD. Snag dynamics models that predict the general rate of fall and decay of snags have been available for several years (Marcot 1992, McComb and Ohmann 1996). These models estimate the number of green trees that need to be retained in harvest units to replace existing snags that will fall during a rotation, and to estimate when to convert green trees to snags. Mortality estimates from growth and yield models can be input into these models to track snag recruitment in forest stands. The Snag Recruitment Simulator (SRS) (Marcot 1992) has been widely used in Land and Resource Management Plans by the USDA Forest Service in the Pacific Northwest.

The main drawback of these models is that they do not assess the dynamics of logs. In order to manage logs through time, it is important to know how they decompose over time. Wright (1998) developed a model that predicted the dynamics of CWD mass through time, although snag and log biomass were aggregated. The

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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objective of our Coarse Wood Dynamics Model (CWDM) is to predict the dynamics of snags and logs as separate entities through time. The CWDM provides output on amounts of CWD, distinguishing between snags and logs of different size and decay classes, every 5 years for a period of up to 300 years.

Model Overview

The CWDM analyzes the dynamics of CWD in forested ecosystems of the western Cascades in Oregon and Washington. The CWDM models Douglas-fir *(Pseudotsuga menziesii)* and western hemlock *(Tsuga heterophylla)* snags and logs. The model predicts snag fall, height loss and decay, and log decay at 5-year intervals for a period of 300 years. Snags either fall whole or partially break off, creating down logs. Snags also decay from hard to soft. Logs decay from sound to decayed conditions, and eventually disappear into the forest floor as duff. The model simulates the decomposition of remnant snags and logs (those existing on site at the beginning of the assessment time) and new snags and logs created from green trees or from mortality. A growth and yield model can be used to determine number and sizes of snags created by suppression mortality. These snags can then be input into the model at the appropriate time during the rotation.

The CWDM follows individual CWD pieces or groups of pieces (same species, size and decay class) through time. The model varies snag fall and height loss rates by species, diameter at breast height (dbh), and decay class. Western hemlock snags fall faster than Douglas-fir snags, and smaller more decayed snags fall faster than larger, sounder snags. Decay is basically the reduction in density of a piece of CWD. Decay rates are different for snags and logs since snags decay faster than logs. The model varies decay of snags and logs by species and size. Western hemlock decays faster than Douglas-fir *(fig. 1).* Smaller snags and logs decay faster than larger ones.

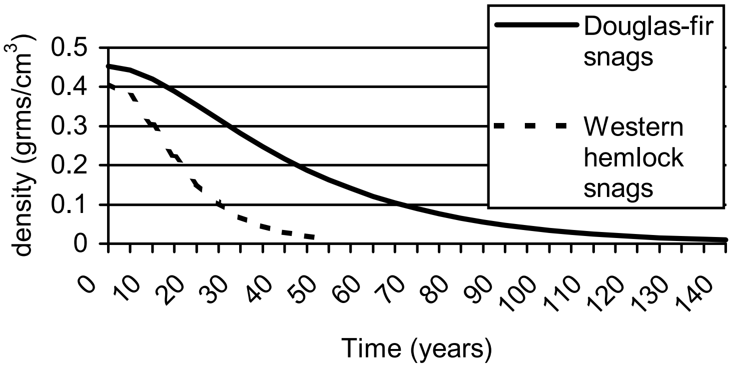

Figure 1—CWDM decay of Douglas-fir and western hemlock snags ranging from 38.1 to 63.5 cm dbh.

Although the current version of the CWDM uses data from the western Cascades of Oregon and Washington, the model could easily be modified to include data from other geographic locations. The same approach taken in the model could also be used to incorporate other species of snags and logs as data become available.

The CWDM is compiled to run in DOS. A Windows version will be released soon.[4] The program and documentation are available from the lead author.

Model Input

CWDM requires input data in the form of two space-delimited ASCII files, one each for snags and logs. The following data are required in the snag input file: year snag created (0 for existing snags), snag species, decay class, dbh (in), height (ft), snags/acre or ha, and site class. The log input includes year log created (0 for existing logs) log species, decay class, large end diameter (in), length (ft), and logs/acre or ha.

A 3-class decay system is used for both snags and logs. Snags are divided into green, hard, or soft snags. Logs are divided into green, sound, or decayed logs. Green snags and logs are those created at the current time either through natural mortality or artificial creation. Hard snags include classes 1-3 and soft snags classes 4 and 5 of the 5-class system developed by Cline and others (1980). Sound logs include classes 1 and 2, while decayed logs include classes 3-5 of the 5-class system developed by Maser and others (1979) for logs.

Model Outputs

The CWDM creates five space-delimited ASCII output files: snagout, logout, snlogout, sumsnags.txt and sumlogs.txt. The first three files are intermediate files that track individual snags or logs through time. The last two are summary files that most users will want to view. The files are sums of snags and logs by time, species, decay class, and dbh or diameter class. Dbh classes for snags are <38.1 cm, 38.1-63.5 cm, and ≥63.5 cm. Diameter classes for logs are <30.5 cm, 30.5-50.8 cm, and ≥50.8 cm. If different dbh or diameter breaks are desired, the snagout and logout files can be imported into a database and for querying.

The fields in sumsnags.txt are time, species, decay class, dbh class, and snags/acre or ha. The fields in sumlogs.txt are time, species, decay class, diameter class, linear feet/acre or ha, and percent cover.

Example Outputs

Figures 2-4 are examples of results from the model. The current version of the CWDM does not produce graphs. Graphic representations can be developed by importing the ASCII files into a spreadsheet or database program with graphing capabilities.

Figure 2 is the result of leaving a mix of species, size, and decay classes of snags on site at time 0. The loss of hard snags is a result of some snags falling and some snags becoming soft. The first increase in the soft snags is when western

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

hemlock snags change from a hard to soft condition. The second increase is from hard Douglas-fir snags becoming soft. The decrease in total numbers of snags is from snag fall.

Figure 3 illustrates the results of recruitment of snags during a time period. In this example a mixture of species, sizes, and decay classes of snags is left at time 0. A few snags are artificially created at years 25 and 50 to replace snags that have fallen. Suppression mortality creates snags ≥ 38.1 cm beginning at year 75. Input from suppression mortality continues until year 95 in this example. Realistically, suppression mortality would continue beyond 95 years, but this is the limit of some growth and yield models.

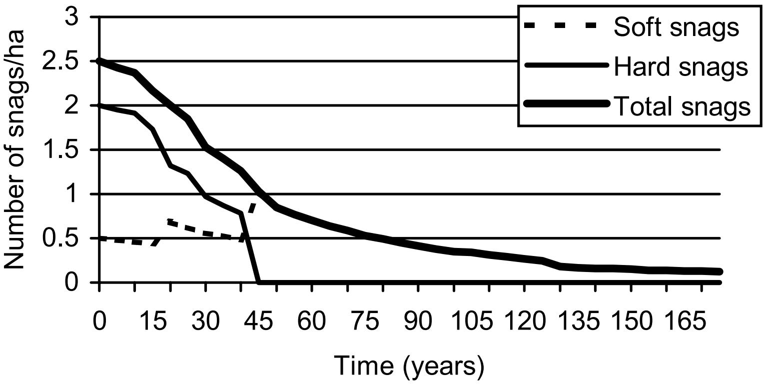

Figure 2—CWDM decrease in the number of snags through time. Loss of total and soft snags is a result of snag fall. Loss of hard snags is a result of decay to the soft decay class and fall. Input at time 0 includes a mixture of hard and soft Douglas-fir and western hemlock snags for a total of 2.5 snags/ha.

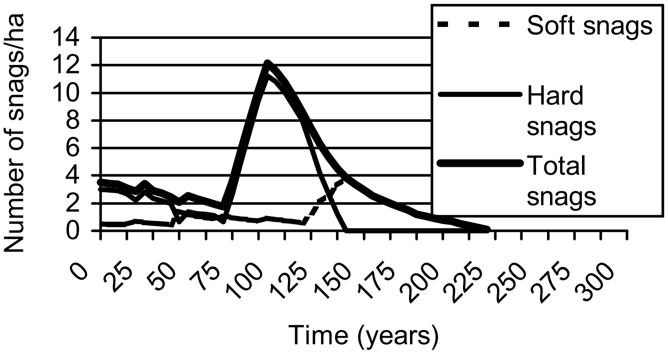

Figure 3—CWDM dynamics of snags through time with recruitment of snags during the rotation. Input at time 0 includes a mixture of hard and soft Douglas-fir and western hemlock snags. Recruitment of snags includes snags artificially created from Douglas-fir trees at years 25 and 50, and from suppression mortality of Douglas-fir trees at years 75, 80, 85, 90, and 95.

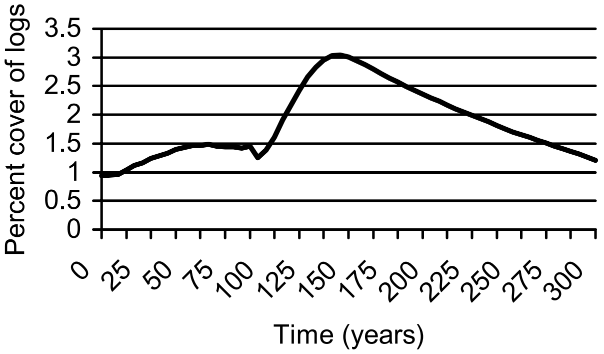

Figure 4—CWDM percent cover of logs through time with recruitment of logs from snags. Input of logs at time 0 is < 1 percent cover. Recruitment of logs through time is all from snags falling as per *figure 3*. Initial input of logs at time 0 includes a mixture of green and sound Douglas-fir and western hemlock logs.

Figure 4 illustrates an example of leaving some sound and green logs on site at time 0 and then incorporates the snags displayed in *figure 3* as they fall partially or whole and become logs. Percent cover of logs is also reduced as they decay.

Assumptions

Given the available data, a number of assumptions were required to develop the model. Foremost is that values for snag and log dynamics reported in the literature are "average." CWD decay is highly variable and highly dependent on site conditions, weather, geographic location, etc. Since the model takes each snag or log and treats it as an average piece on an average site, the model outputs should be considered as general guidelines and should be applied over larger areas or landscapes.

Because data for western hemlock are very limited, we used more substantial data for Douglas-fir to develop size-specific values used for western hemlock decay and fall rates. It is clear from data that are available that western hemlock CWD falls and decays much faster than Douglas-fir CWD.

The model assumes snags fall at a constant rate over time, varying only by dbh and decay class. In reality snags probably are created and fall in "pulses" over time. The pulses are difficult to predict and thus are not incorporated in the model. This omission should have little effect on the ability of the CWDM to predict the general dynamics of CWD levels throughout a rotation or planning cycle.

It is assumed that there is a lagtime once a green tree becomes a snag before it begins to decay and fall. Lagtimes were applied to snags created from green trees.

Several assumptions were made regarding the process by which snags break and fall. It was assumed that snags often break and fall in two to three pieces, although some snags also fall whole. At any one time, some snags will lose a portion of their original height. Height loss was averaged for snags. Based on Pacific Northwest Research Station (PNW) Forest Inventory and Analysis (FIA) program data, it was assumed that on average one-third of a snag falls when it loses height. Taper equations were used to determine two-thirds height diameter of snags to determine large end diameter of the log. To calculate the number of log pieces, we assumed that 27 percent of standing snags lost a portion of their height over a 5-year period (based on FIA data). Class 5 snags that fall are not counted as logs. They were assumed to disintegrate and contribute to the duff layer.

For snags it is assumed that volume (m^3/ha) is constant except for the portion of snag height that breaks off during the time period. As snags move toward decay class 5 this assumption is probably violated, as dbh is also reduced by fragmentation of the snag. As a result, calculations for very soft snags probably underestimate density.

For Douglas-fir logs it was assumed that volume is constant until the log reaches the class 4 decay stage (Graham 1982). Volume of class 4 and 5 logs is "decayed" using fragmentation rates. Fragmentation rates were obtained from Graham (1982). Diameter and length of logs were also reduced for decay class 4 and 5 logs based on Maser and Trappe (1984). Western hemlock logs do not fragment like Douglas-fir because bark remains intact, forming a protective shell around the log (Graham 1982).

It was assumed that, on average, existing snags and logs are halfway through either the hard or soft decay class for snags or sound or decayed class for logs. Densities were assigned based on midpoint densities of either the hard or soft decay class.

Decay rates were applied to biomass in equations in the CWDM. Decay rates are a combination of mineralization and fragmentation of boles. Both types of decay reduce biomass: mineralization reduces density, and fragmentation reduces volume. In the model the two types of decay were usually combined. In the case of decayed logs, fragmentation rates were applied to the log volume.

The Smalian formula (Wegner 1984) was used to calculate volume. This volume is then multiplied by decay class specific density to get biomass. Because the Smalian formula tends to overestimate volume by about 10 percent (Wegner 1984), biomass is overestimated. This is not a problem with the decay equations in the model because decay is relative; thus, differences in biomass do not influence rate of decay. However, biomass and volume results should not be used as the absolutes for CWD in a stand.

Data Sources

Information on decay rates *(tables 1, 2)* was gleaned from the literature. Decay rates for Douglas-fir snags are from Graham (1982). Decay rates for Douglas-fir logs are from 3 sources: decay rates for logs >38.1 cm diameter are from Graham (1982); decay rates for logs 15.2-38.1 cm diameter are from Means (in Harmon and others 1986); and decay rates for logs < 15.2 cm diameter are from Erickson and others (1985).

Less data are available for decay of western hemlock. An overall decay rate for logs and snags is given by Graham (1982), but size-specific decay rates are not available. Decay rates for three size classes are extrapolated based on comparative fall rates of snags in the different size classes. It was assumed that fall rates indicated relative fragmentation rates. The logic was checked by trying the same extrapolation with Douglas-fir snags and comparing to reported decay rates. The result was close;

extrapolated decay rates were within 0.003 (or 85 percent). Decay rates for largest logs are extrapolated based on Douglas-fir decay rates. Decay rates for logs <15.2 cm diameter are from Erickson and others (1985).

Table 1—*Snag decay rates used in the CWDM.*

Species[1]	Dbh class (cm)	Decay rate (k)	Decay lagtime[2] (years)	Lagtime decay constant[2]
DF	≥ 63.5	0.017	20	0.06
DF	38.1 – 63.5	0.033	15	0.14
DF	< 38.1	0.053	10	0.25
WH	≥ 63.5	0.060	15	0.15
WH	38.1 – 63.5	0.088	10	0.25
WH	< 38.1	0.100	5	0.30

[1] DF = Douglas-fir; WH = western hemlock

[2] Decay lagtime and constant applied to newly created snags only.

Table 2—*Log decay and fragmentation rates used in the CWDM.*

Species[1]	Diameter class (cm)	Decay rate (k)	Fragmentation rate[2] (kf)	Diameter reduction rate[2] (rd)	Length reduction rate[2] (rl)
DF	≥ 38.1	0.012	0.008	0.0031	0.0026
DF	15.2 – 38.1	0.015	0.010	0.0037	0.0030
DF	<15.2	0.026			
WH	≥ 38.1	0.019			
WH	15.2 – 38.1	0.023			
WH	<15.2	0.030			

[1] DF = Douglas-fir; WH = western hemlock

[2] Fragmentation, diameter reduction and length reduction rates apply to class 4 and 5 Douglas-fir logs only.

Snag fall and height loss rates *(table 3)* are based on remeasurement data from snags on private lands. The data were collected through the PNW FIA program.[5] The snags were measured in the late 1970s and again in the late 1980s. Presence or absence of snags were noted, and changes in height and decay class were recorded. Using FIA data, snags that disappeared during the 10-year remeasurement period are assumed to have fallen whole. The 10-year fall and height loss rates were converted to 1-year rates. Fall and height loss rates were averaged for size class (<38.1, 38.1-63.5, ≥63.5 cm dbh) and decay class (hard vs. soft) *(table 3).* Size and decay classes were lumped if there was no significant difference (alpha=0.20) in rates of fall or height loss. A large alpha value was used because the effect of a type 1 error was considered less risky to the outcome of the model than a type 2 error. Sample sizes are small and data are variable, but the trends in the data supported what is known from other data about relative fall rates of snags.

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[5] Unpublished data on file, Pacific Northwest Research Station, Janet Ohmann, Portland, Oregon.

Table 3— *Snag fall rates and height loss proportions used in CWDM.*

Species[1]	Diameter class (cm)	Decay class[2]	Fall rate (p)	Height loss proportion (p)	Fall lagtime[3]
DF	≥ 63.5	Hard	0.008	0.019	15
DF	≥ 63.5	Intermediate	0.008	0.019	
DF	≥ 63.5	Soft	0.008	0.019	
DF	38.1 – 63.5	Hard	0.013	0.033	10
DF	38.1 – 63.5	Intermediate	0.022	0.038	
DF	38.1 – 63.5	Soft	0.027	0.041	
DF	< 38.1	Hard	0.021	0.042	0
DF	< 38.1	Intermediate	0.043	0.056	
DF	< 38.1	Soft	0.054	0.063	
WH	≥ 63.5	Hard	0.01	0.024	5
WH	≥ 63.5	Intermediate	0.017	0.029	
WH	≥ 63.5	Soft	0.021	0.031	
WH	38.1 – 63.5	Hard	0.02	0.035	0
WH	38.1 – 63.5	Intermediate	0.03	0.044	
WH	38.1 – 63.5	Soft	0.035	0.048	
WH	< 38.1	Hard	0.03	0.035	0
WH	< 38.1	Intermediate	0.039	0.044	
WH	< 38.1	Soft	0.044	0.048	

[1] DF = Douglas-fir; WH = western hemlock

[2] Decay classes reflect groups of the 5-stage system developed by Cline and others (1980). Hard = 1 and 2 =; Intermediate 3; Soft = 4 and 5.

3 Fall lagtimes applied to newly created snags only.

The sharp change in fall and height loss rates between hard and soft snags caused calculation problems for the model because snags gained height as they went from hard to soft. As a result, intermediate fall and height loss rates are applied to class 3 snags *(table 3).* Since there are 3 classes in the broad category of "hard," two-thirds of the difference between hard and soft fall and height loss rates is added to the "hard" class rates to determine intermediate rates for class 3 snags. Using intermediate rates smoothes the decay curves but does not change the long-term decay and fall of snags.

Lagtimes for beginning of snag decay and fall *(tables 1, 3)* are from Cline and others (1980) and Harmon and others (1986). Data on lagtimes for western hemlock snags are not dbh specific. Lagtimes for the 3 dbh classes are based on extrapolating the relationship of increase in lagtime with increase in dbh for Douglas-fir snags and applying the extrapolation to western hemlock snags.

Taper equations from Walters and Hann (1986) are used to calculate top and mid-height diameter of snags. Mid-height diameter is needed to determine large end diameter of logs created as snags break. Both diameters are used in volume calculations. The taper calculations require knowing the height and crown ratio of the tree before it became a snag. Forest Service Continuous Vegetation Survey (CVS) data from the Mt. Hood and Gifford Pinchot National Forests were used to determine average height and crown ratio of trees of a given dbh on low, moderate, and high sites.[6] Only data on live trees without broken or deformed tops were used for the

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[6] Unpublished data on file, Pacific Northwest Region, Portland, Oregon.

estimates of height and crown ratio. Average height was calculated for 12.7 cm-dbh classes up to 101.6 cm dbh and by 25.4 cm-dbh classes for dbh greater than 101.6 cm. Height and crown ratio were determined for dbh classes of <38.1 cm, 38.1-63.5 cm and $\geq$63.5 cm. Only significant differences (alpha =0.05) were used; otherwise, height and crown ratio were averaged over two or more dbh classes. Plant associations (Brockway and others 1983, Halverson and others 1985, Hemstrom and others 1982, Topik and others 1986) were used to determine if data were from high, moderate, or low sites. High and moderate sites were in plant association where average growth was $\geq$ 6 m^3/ha/year. Growth on low sites was < 6 m^3/ha/year. Because there was no significant difference between height crown ratio on high and moderate sites, data for those sites were lumped.

The Walters and Hann (1986) equations used for calculating taper for snags can not be used directly on logs, because large end diameter does not necessarily relate to dbh of a tree that is needed to calculate taper. Data Jane Kertis and Mark Huff [7] on log length and small end and large end diameters, were used to determine small end diameter of logs given large end diameter and length. The data are from the Willamette National Forest in the western Oregon Cascades. Small end/large end ratios were calculated for each log. Simple linear regression was used to determine the relationship between log length and the small end/large end ratio. For Douglas-fir logs, sound and decayed logs were assessed separately. For western hemlock logs, sound and decayed logs were combined. Class 5 logs were not used in the equations. The regressions were highly significant with the following *P*-values: Douglas-fir = 9.93 E-33; western hemlock = 5.33 E-10.

Densities of snags and logs (g/cm^3) *(tables 4-7)* are needed to convert volume to biomass for the decay equations and to determine decay class of snags and down logs. Densities for both Douglas-fir and western hemlock class 1-5 snags and logs are from Spies and others (1988). Densities for green snags and logs are from Harmon (1992).

Snags and logs are removed from the model when they reach a maximum age *(tables 4-7)*. Maximum age of Douglas-fir snags is from Cline and others (1980). Maximum ages for all logs and western hemlock snags are from Graham (1982) and half-life data are from Harmon and others (1986).

Table 4—*Density and ages for decay classes of Douglas-fir snags used in the CWDM. Values are for snags as they first enter a decay class. Ages are based on output from the model.*

		Dbh class (cm)		
Decay class	**Density (gm/cm^3)**	**$\geq$ 63.5**	**38.1 – 63.5**	**< 38.1**
		Snag ages (yrs)		
1	0.452	0	0	0
2	0.380	15	15	15
3	0.284	35	30	25
4	0.197	60	45	30
5	0.140	80	60	40
Maximum age		250	130	75

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[7] Unpublished data on file, Willamette National Forest, Jane Kertis and Mark Huff, Eugene, Oregon.

Table 5—*Density and ages for decay classes of western hemlock snags used in the CWDM. Values are for snags as they first enter a decay class. Ages are based on output from the model.*

		Dbh class (cm)		
Decay class	**Density (gm/cm^3)**	**≥ 63.5**	**38.1 – 63.5**	**< 38.1**
		Snag ages (yrs)		
1	0.408	0	0	0
2	0.348	10	10	5
3	0.263	20	15	10
4	0.215	25	20	10
5	0.138	30	25	15
Maximum age		85	50	35

Table 6—*Density and ages for decay classes of Douglas-fir logs used in the CWDM. Values are for logs as they first enter a decay class. Ages are based on output from the model.*

		Diameter class (cm)		
Decay class	**Density (gm/cm^3)**	**≥ 38.1**	**15.2 – 38.1**	**< 15.2**
		Log ages (yrs)		
1	0.452	0	0	0
2	0.380	15	15	10
3	0.284	40	35	20
4	0.197	70	60	35
5	0.140	155	115	45
Maximum age		315	245	70

Table 7—*Density and ages for decay classes of western hemlock logs used in the CWDM. Values are for logs as they first enter a decay class. Ages are based on output from the model.*

		Diameter class (cm)		
Decay class	**Density (gm/cm^3)**	**≥ 38.1**	**15.2 – 38.1**	**< 15.2**
		Log ages (yrs)		
1	0.408	0	0	0
2	0.348	10	10	10
3	0.263	25	20	15
4	0.215	35	30	25
5	0.138	60	50	40
Maximum age		95	75	60

Calculations

Equations

The following are the equations used to calculate parameters in the CWDM:

Parameter	**Equation**
Volume	
snags[1]	volume = ((Ab+At)/2)*L
logs (1-3)[1]	volume = ((Ab+At)/2)*L
logs (4-5)[2]	current volume = initial volume*(EXP(-kf(t-tIV)))
Decay	
green snags[3]	current biomass = initial biomass*(1-(1(EXP(-kt))$^{(lt*lc)}$
hard/soft snags[4]	current biomass = initial biomass*(EXP(-kt))
logs[4]	current biomass = initial biomass*(EXP(-kt))
Snag fall[5]	current snag/ha = original snag/ha*(EXP(-pt))
Snag height loss[6]	current height = original height*$(1-p)^t$
Log diameter[7]	current diameter = initial diameter*(EXP(-rd(t-tIV)))
Log length[8]	current length = initial length*(EXP(-rl(t-tIV)))
Log taper[9]	small end diam. = large end diam.*(Yintercept+(slope*L))
Log pct. cover[10]	Pct. cover = (((le diam*L)/2)+((se diam*L)/2))/100

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[1] Smalian equation from Wegner (1984); Ab=area of base or large end; At=area of top or small end; L=snag height or log length.

[2] kf=fragmentation rate (see *table 2*); t=time elapsed; tIV=time at which logs becomes a class 4.

[3] Green snags are those created at the current time; k=decay rate (see *table 1*); t=time elapsed; lt=lagtime; lc=lagtime constant; see table 1 for lagtime and lagtime constant.

[4] Snags that are hard or soft at the beginning of the planning cycle; k=decay rate (see *tables 1* and *2*); t=time elapsed.

[5] p=proportion of snags falling per year (see *table 3*); t=time elapsed; applied after lagtime has elapsed.

[6] p=proportion of height lost per year (see *table 3*); t=time elapsed; applied after lagtime has elapsed.

[7] rd=diameter reduction rate (see *table 2*); t=time elapsed; tIV=time at which logs becomes a class 4.

[8] rl=length reduction rate (see *table 2*); t=time elapsed; tIV=time at which logs becomes a class 4.

[9] L=length; for Douglas-fir Yintercept=0.884, slope=-0.0044; for western hemlock Yintercept=0.902, slope=-0.0055; small and large end diameter and length are used in calculations for volume and percent cover.

[10] le diam=large end diameter (in); se diam=small end diameter (in); L=length (ft)

Discussion of Calculations

A lagtime decay equation is used for snags created from green trees to account for a lag between death of a tree and the beginning of decay. The equation is from Harmon and others (1986). Lagtime constants were determined by trial and error. Constants that resulted in a decay curve that approximated those in Cline and others (1980) were used.

When modeling decay of snags created from green trees, the results indicate that biomass lost during the lagtime was all due to mineralization. In reality, some snags probably break or fall, but very few due to lagtime for falling. Lagtime equations similar to the one used for decay did not work for fall and height loss calculations. The curves became too steep and didn't match fall rates (Cline and others 1980). Thus, absolute lagtimes are used. It is assumed that no snags fall during the lagtime.

Rates for reduction of log diameter and length are from Maser and Trappe (1984). Length of Douglas-fir logs decreases 55 percent between class 1 and class 5, and diameter is reduced by 68 percent, mostly due to bark loss. Rates (rd and rl) are calculated by taking the number of years to get halfway between the beginning of the class 5 condition and the maximum life of the log and then dividing the percent reduction by that number of years.

The density at which a snag changes from hard to soft was determined by bracketing the average densities for the decay classes 3 and 4 by the standard deviation of the density estimate. The density at which the upper bracket of class 4 and lower bracket of class 3 meet is used as the density that triggers classifying the snag as hard or soft *(tables 4, 5).* Each snag was tracked through time, and as decay class changed the decay-specific fall rates were applied. The density at which logs go from sound to decayed was calculated in a manner similar to that for snag calculations except that class 2 and 3 densities were used *(tables 6, 7).*

Densities for existing snags are assigned based on midpoint densities of either the hard or soft decay class. The midpoint density of hard snags was calculated by averaging densities for class 3 and green tree densities. The midpoint density for soft snags was calculated by averaging densities for class 4 and 5 snags. The midpoint density for sound logs was calculated by averaging densities for class 2 and green tree densities. The midpoint density for decayed logs was calculated by averaging densities for class 3 and class 5 logs.

Model Validation

Data from Cline and others (1980) were used to validate the fit of the model for Douglas-fir snags against the decay rates used in the model (Graham 1982). Age at which a snag went from hard to soft for different dbh classes and the maximum life of snags from the CWDM was validated against data in Cline and others (1980). Because dbh breaks did not match exactly between the two studies, generalized extrapolations were made. Data were not available to validate western hemlock snag decay and fall.

For logs, decay rates and equations in the model were tested against age range for each decay class in Graham (1982). This is not a true validation because decay rates and ages came from the same data set—it just validates that the equations and values used were producing the expected results. Half-lives from two additional datasets (reported in table 3 of Harmon and others 1986) were also used to help validate decay rates. Data from Sollins and others (1987) were used to check the log decay rate against ages of logs in decay classes 1 to 4.

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Snag Recruitment in Subalpine Forests of the North Cascades, Washington State[1]

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Abstract

We recorded snag species, locations, and causal agents of tree mortality, and estimated fire histories and standing dead and downed fuel abundance in polygons in subalpine forests in the Entiat watershed in Washington State. The overall snag density was 51 ± 5.2 snags per hectare. The density of dominant and codominant snags did not differ by aspect or slope categories ($p = 0.74$), but the density of intermediate and suppressed snags was highest on steep south-facing slopes ($p < 0.05$). Weather-related effects created more snags than any other disturbance in the period between stand-replacing fires. More weather-caused mortality occurred on northerly aspects than on southerly aspects ($p < 0.05$) and on mid-slopes than either upper or lower slopes ($p < 0.05$). Standing dead and downed fuel, and tree mortality caused by weather (snow, ice, and wind), root diseases, animals, and bark beetles were related to stand structural stage. We estimate the mean fire interval was 12 years for the 5,685 ha encompassed in the study area. The estimated mean size of stand-replacing fires was 146 ± 95 ha.

Introduction

Vegetation in subalpine forests is not distributed randomly but is closely tied to topography, climate, and the cumulative effects of disturbances at various scales. Disturbance regimes of subalpine forests differ considerably from those of forests at lower elevations where fire was historically a frequent visitor to all stand development stages, commonly burning large areas at low severity and selectively killing individuals and small groups of trees. In contrast, fires in subalpine forests are less common and are typically mixed-severity or stand-replacing (Covington and others 1994).

How a tree dies influences its longevity as a snag and its usefulness to wildlife (Bull and others 1997). Snag longevity is site-specific (Everett and others 1999, Keen 1929) and is enhanced by larger bole diameter, shorter height, and thinner bark (Raphael and Morrison 1987). When killed by fire, thin-barked species such as Engelmann spruce *(Picea engelmannii* Parry ex Engelm.), lodgepole *pine (Pinus contorta* var. *latifolia* Dougl. ex Loud.), and subalpine fir (*A. lasiocarpa* [Hook] Nutt.) dry quickly (Bull 1983), making them resistant to insects and decay fungi

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(Hadfield and Magelssen 1997, Parry and others 1996) and increasing their longevity as snags (Everett and others 1999).

Over the course of stand development, insects and pathogens kill far more trees and recycle more biomass in most forests than do fires (Hagle and others 1995). With the exception of large-scale outbreaks of the mountain pine beetle *(Dendroctonus ponderosae* Hopkins) and spruce beetle (*D. rufipennis* Kirby), most of the conifer mortality caused by biotic agents in subalpine forests occurs individually or in small groups. The slow accumulation of fuel beds and fuel ladders resulting from insect and pathogen activity, as well as by wind, snow, and animals, takes place over a long period of time but affects the behavior of subsequent fires.

Methods

The study site is located in subalpine forests of the Entiat Ranger District, Wenatchee National Forest, on the eastern slope of the Washington Cascade Range *(fig. 1)*. The study site was chosen because the range of climatic and vegetation conditions are representative of many other sites in the Cascade Mountains of eastern Washington State. Elevations in the study area range from 1,280 m to 2,150 m above sea level. Mean annual precipitation in the study area ranges from approximately 100 to 230 cm. Subalpine forests in the upper Entiat watershed are classified into five major plant series: whitebark pine (*Pinus albicaulis* Engelm.), subalpine larch (*Larix lyallii* Parl.), subalpine fir, mountain hemlock *(Tsuga mertensiana* [Bong] Carr.), and Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) (Lillybridge and others 1995). The western-most forests in the study area are in the Glacier Peak Wilderness Area. Plummer (1902) commented on burns that occurred in the 1800s: "On the high divides between Entiat and Mad Rivers extensive burns occurred years ago, and the very life was burned out of the soil, leaving it poor indeed."

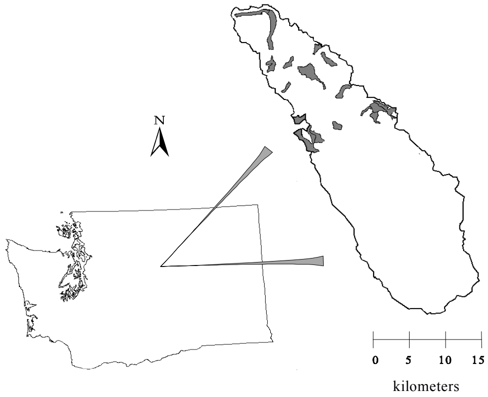

Figure 1—Location of study sites (shaded gray) in the Entiat watershed, Washington State.

Black and white aerial photographs taken in 1992 at a scale of 1:16,000 were used to delineate polygons. Eighteen polygons representing several predominant aspect and slope categories were randomly selected from a total of 93, allotting 3 polygons to each slope and aspect category. The total area encompassed by the 18 selected polygons was 5,685 ha; the average size was 316 ha ± 181 ha. Stand types within polygons were subjectively classified by crown density and whether crowns had single or multiple layers. Aerial photographs were also used to assign stand types to one of seven structural stages: stand initiation, open stem exclusion, closed stem exclusion, understory reinitiation, young multi-strata, old forest multi-strata, and old forest single-stratum (O'Hara and others 1996, Oliver 1981). Less than 1 ha in the study area was classified as old forest single-stratum. Therefore, data from old forest single-stratum and old forest multi-strata were combined. Polygon and stand type boundaries were drawn on 1:24,000 scale USDA Forest Service resource orthophotos then digitized into a geographic information system.

Fire histories, occurrences, and extents were estimated from a variety of sources. Ages of the oldest appearing conifers in each stand type were measured. Fire atlases, which are maps with boundaries of fires hand-drawn at the time of occurrence, historical panoramic photographs taken from fire lookouts, and aerial photographs supplemented stand age data and improved estimates of fire sizes. The most recent fires were mapped for each polygon. FHX2 fire history software (Grissino-Mayer 1995) was used in this study to calculate the Weibull median fire interval (*sensu* Johnson and Gutsell 1994) for the area encompassed by the 18 polygons.

Downed and dead woody fuel was measured in tones per ha using the planar intersect method (Brown 1974) at plot centers. Sampling plane lengths varied from 0.9 m for continuous heavy slash of 0 to 2.54 cm to 11 m for light slash larger than 15 cm.

Both belt transects and fixed area plots were used to collect data on conifer mortality. Five variable-length 9.1 m belt transects were systematically established in each polygon to cross all stand type, beginning and ending at polygon boundaries. The following data were recorded in each transect: extents of stand types encountered; conifer species and crown class for each dead tree. Crown classes were assigned to individual trees according to Oliver and Larson (1990). All agents potentially contributing to mortality were recorded for each dead tree, and a determination was made of the primary agent responsible. For example, the primary agent recorded for a tree with evidence of moderate to aggressive root disease and bark beetle galleries was root disease. Trees that were blown over were recorded as killed by weather. Some of these may have been infected by root disease. Trees with advanced root disease are more likely to fail than trees with intact root systems (Harvey and Hessburg 1992). Fixed circular 0.02 ha plots were established where a belt transect crossed closest to the center of each stand type. Diameter at 1.37 m, henceforth referred to as dbh (diameter at breast height), and crown position were recorded for every live and dead tree in each fixed plot. Statistical tests were performed using Statistical Analysis Systems software (SAS 1997).

Results and Discussion

Subjective data from fire atlases, historical panoramic photographs from fire lookouts, and aerial photographs were analyzed, as were 793 tree age cores. Forty-one fires were recorded, dating from 1505 to 1935. The most recent fire in 14 of the 18 polygons occurred between 127 and 102 years ago. Between 1880 and 1900, over half of the polygons had a fire that burned at least 25 percent of the area, equivalent to 2,126 ha. The Weibull mean fire interval was 12 years for the 5,685 ha encompassed in the study. Intervals between fires on the same polygon varied from

10 years to 291 years, and it is likely that fires did not overlap much in extent. The estimated mean size of stand-replacing fires was 146 ha (standard error [s.e.] = 95 ha). Lightning directly killed 4 trees, and small lightning-caused fires killed an additional 68 trees.

Downed and dead fuel weight from 116 planar transects were compared to stand structural stage *(fig. 2)*. Eight of the 15 possible two-way comparisons differed statistically (as indicated by standard error bars).

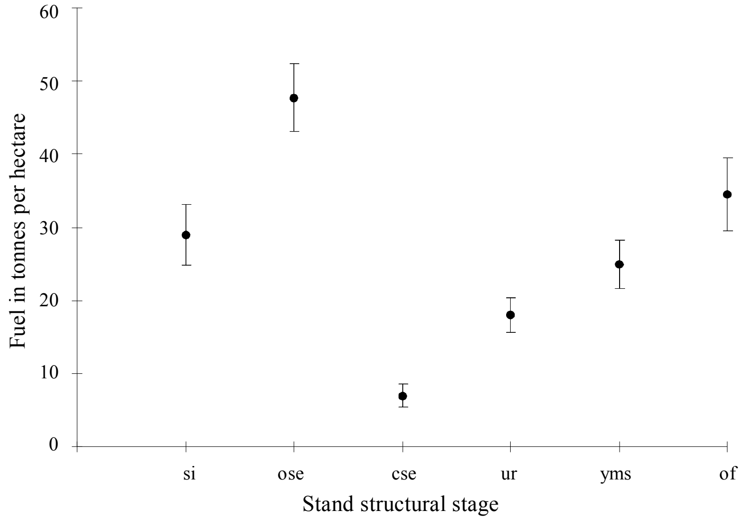

Figure 2—Dead and downed fuel by stand structural stage: si = stand initiation, ose = open stem exclusion, cse = closed stem exclusion, ur = understory reinitiation, yms = young multistory, of = single stratum and multi-stratum old forest. Vertical lines are standard errors of the mean.

A total of 6,629 snags (standing dead trees), were recorded along 142 km of belt transects, representing a 130 ha sample size. The overall snag density was 51 ± 5.2 snags per ha. An additional 329 snags were recorded in the 77 fixed plots in the 18 polygons. Snags were combined into two groups based on similarities in crown class: dominant and codominant snags, and intermediate and suppressed. The majority of the snags (83 percent) at one time occupied dominant or codominant crown positions relative to the surrounding trees. Mean dbh for dominant and codominant snags was 32.5 cm (s.e. = 17.6). Mean dbh for intermediate and suppressed snags was 14.1 cm (s.e. = 10.8).

The number of intermediate and suppressed snags per ha was significantly higher ($p < 0.05$) for steep (> 50 percent) south-facing slopes, which had a preponderance of relatively pure, dense lodgepole pine stands, than for other slope and aspect categories *(table 1).* The number of dominant and codominant snags per ha did not differ significantly by aspect and slope categories ($p = 0.74$). Mean basal area in vegetation plots was 43 m^2 per ha (n = 115; s.e. = 98).

Table 1—*Snags per hectare by aspect and slope in two crown class categories.*

	Slope (percent)					
	10-30		30-50		50+	
Aspect	DC[1]	IS	DC	IS	DC	IS
North	36	5	36	7	47	7
South	47	3	48	9	51	37[2]

[1] DC = dominant + codominant, IS = intermediate + suppressed

[2] Significantly different than other aspect/slope combinations for intermediate and suppressed trees.

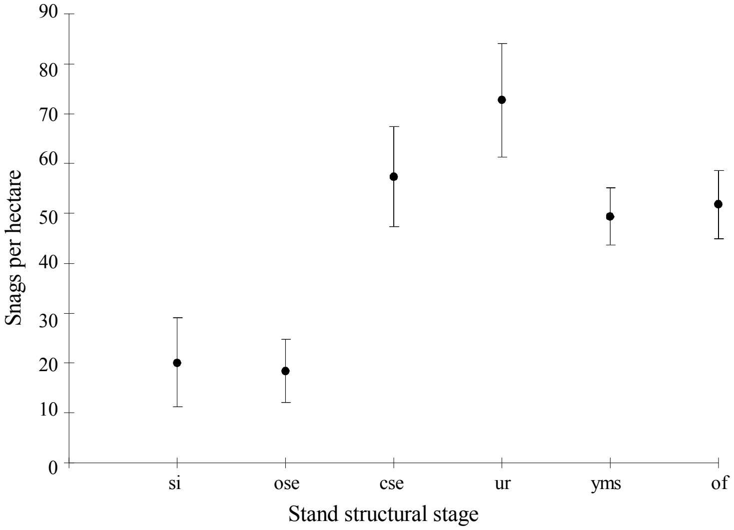

Figure 3—Snags per hectare by stand structural stage: si = stand initiation, ose = open stem exclusion, cse = closed stem exclusion, ur = understory reinitiation, yms = young multistory, of = single stratum and multi-stratum old forest. Vertical lines are standard errors of the mean.

Snag density was significantly different ($p < 0.01$) among the 6 structural stand stages for both the dominant and codominant snag category and the intermediate and suppressed snag category. A majority of the total snags (88 percent) were found in four structural stand stages: closed stem exclusion, understory reinitiation, young multi-story, and old forest *(fig. 3)*.

Conifer mortality by crown class was analyzed for Engelmann spruce, subalpine fir, whitebark pine, and lodgepole pine. Disturbance groups included in the analyses were weather, bark beetles, root diseases, animals, white pine blister rust (*Cronartium ribicola* Fisch.) in whitebark pine and lodgepole dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) in lodgepole pine. All four conifer species analyzed had the majority of mortality in dominant and codominant crown classes, regardless of the disturbance agent species or group ($p < 0.05$).

Snow, ice, and wind created significantly more snags than insects, pathogens, animals, or fire. A majority of these snags were subalpine fir and lodgepole pine broken off at, or near, the base of the live crown. Only weather-caused tree mortality showed a difference by aspect or slope categories. More weather-caused tree mortality occurred on northerly aspects than on southerly aspects ($p < 0.05$), and on mid slopes than on either upper or lower slopes ($p < 0.05$). The mid-slope on a mountain, also called the thermal belt, typically receives the least variation in diurnal temperature, has the highest average temperature, and the lowest average relative humidity (Anonymous 1981). Therefore, fuels in the study area were most likely to accumulate where they would dry quickest and have the lowest fuel moisture. The trend in old forest structures is for fewer weather-killed trees than in the intermediate structural stages. This might be attributable to the decreased number of trees overall in old forest.

The second and third most common disturbance agents were bark beetles and root diseases, respectively. Lodgepole pine was the tree species most commonly killed by bark beetles. In the study area, most stands of lodgepole pine were very dense, and were attacked not by mountain pine beetles but by secondary bark beetles such as *Pityogenes* spp. and *Pityophthorus* spp., sometimes in concert with Armillaria root disease. Armillaria root disease killed nine different conifer species in the study area, accounting for 88 percent of the mortality caused by identified root diseases. Fifteen percent of the subalpine fir, 41 percent of the Engelmann spruce, and 51 percent of the lodgepole pine infected with root disease were also attacked by bark beetles.

Stand replacement fires create pulses of snags on the landscape. The number of standing dead trees per ha was compared to the time since the last stand-replacing fire for four disturbance agent groups: weather, bark beetles, root disease, and animals. The correlation for each group was not significant, indicating that just using time since the last fire is inadequate in predicting conifer mortality from these disturbance agent groups. Structures and compositions of the previous stands are unknown, as are the intensities and severities of the last fires. These variables, if known, might result in better correlations with conifer mortality in the current stands. Also, in stands where the last fire date was estimated, the range in number of years (62 to 127) since the last fire may be inadequate to demonstrate consistent differences in insect- and pathogen-induced mortality.

The highest standing dead fuels were found in intermediate structural stages *(fig. 3),* and the highest downed and dead fuels are found in the earlier structural stages and in old forest structure *(fig. 2).* Perhaps this is carryover from stand replacement events. Conifer mortality begins to increase in intermediate structural stages, primarily from wind, snow, ice, root diseases, and bark beetles. Wood decay rates are relatively slow in the eastern Cascade Mountains due to climatic factors, and as a result fuels increase faster than they decompose.

In subalpine forests in Rocky Mountain National Park, Clagg (1975) found that total dead woody fuels increased immediately after a fire, quickly declined to a low point at about a stand age of 50 years, rapidly increased to a peak at 100 years, then gradually declined until about age 300 years, after which the fuel load remained almost constant. In a subalpine watershed in Yellowstone National Park, Romme (1982) found that heavy down fuel decreased during early successional stages between stand ages 70 and 200 years as large fire-killed stems decomposed, then fuels increased in later stages when natural mortality of mature trees began to occur. Maximum fuel loading was reached around 350 years.

The average fire size was 146 ha ± 95 ha. Current tree harvest units do not mimic these sizes or their variability. The legal limitations imposed on sizes of harvest units conflict with the size of inherent disturbance regimes, and with the intent of ecosystem management. By targeting mid-slopes where lodgepole pine is dominant and where subalpine fir is increasing in the understory, multiple-use goals can be achieved. On these sites, thinning lodgepole pine and cutting subalpine fir would produce larger trees for wildlife and eventual harvest, increase resistance to bark beetles and weather (e.g., wind), and decrease potential dead and down fuel. The tradeoff is a short-term increase in fuels from logging slash.

In the last half of this century, subalpine forests have become more uniform and dense (Covington and others 1994, Tande 1979), and have greater vulnerability to stand-replacing fire (Romme and Despain 1989). In the Northern Cascades Ecological Reporting Unit of the Columbia River Basin, there were no significant changes in fuel loading among fuel classes from the historical to the current period. Similarly, in the Wenatchee subwatershed, there were no significant changes in fuel loading from the historical to the current period (Huff 1995). However, in the Wenatchee subwatershed, there was a significant decrease in the number of forested stands with no dead trees, and a significant increase in the number of forested stands with from 1 to 10 percent dead trees (Lehmkuhl and others 1994). In this study, standing dead trees were more numerous than required for four species of woodpeckers, according to one study (Thomas and others 1979). Although some species of wildlife may currently benefit from the bounty, fuels and flammability of these forests are increasing, and the inevitable stand-replacing fires may be larger and more severe than were historical fires.

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DecAID: A Decaying Wood Advisory Model for Oregon and Washington[1]

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Abstract

DecAID is a knowledge-based advisory model that provides guidance to managers in determining the size, amount, and distribution of dead and decaying wood (dead and partially dead trees and down wood) necessary to maintain wildlife habitat and ecosystem functions. The intent of the model is to update and replace existing snag-wildlife models in Washington and Oregon. Whereas the relationship of dead and decaying wood to wildlife habitat is a major component of the model, DecAID will also provide expert advice on prescribing and interpreting conditions of dead wood for wildland and prescribed fire and fuels, pest and non-pest insects, pathogens and non-pathogenic fungi, and use of inventory data to describe current managed and natural levels of dead wood. The model also produces a list of ecosystem functions performed by species associated with dead and decaying wood. Advice on the distribution of dead wood at the stand and landscape scale is provided in the model.

Introduction

Models have been developed in the past to provide managers with tools by which they can determine snag sizes (diameter at breast height or dbh) and densities (number of snags per unit area) needed to maintain snag-dependent wildlife. These models focus on needs of primary cavity excavating species of birds (woodpeckers, nuthatches, and chickadees) (Neitro and others 1985, Thomas and others 1979). No similar models have been developed for down wood, largely because until recently there have been no empirical data relating wildlife species and population densities to

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down wood conditions and amounts in Oregon and Washington. Our new model, DecAID (Decayed Wood Advisory Model), is intended to replace the currently used models for determining snag numbers. DecAID will help resource specialists determine how to manage for the amount, type, and distribution of all types of dead wood within forest stands and across landscapes.

DecAID is being developed as part of an update to the existing wildlife habitat relationships books for Washington and Oregon (Brown 1985, Maser and others 1984, Thomas 1979) in a new book entitled *Wildlife-Habitat Relationships in Oregon and Washington,* hereafter referred to as the Species-Habitat Project (SHP). The Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife are leading this effort. The USDA Forest Service is a major partner. DecAID is a work in progress; this paper is a report on the current status of the model (Marcot and others 2002, Ohmann and Waddell 2002).

Existing Models

Existing models of the relationships between wildlife species and snags in the Pacific Northwest typically are based on calculating potential densities of bird species and expected number of snags used per pair. This approach was first used by Thomas and others (1979). Marcot expanded this approach in Neitro and others (1985) and in the subsequent Snag Recruitment Simulator (Marcot 1992) by using published estimates of bird population densities instead of calculating population densities from pair home range sizes.

Recently there has been criticism of the existing modeling approach, in part because the numbers of snags suggested by the models seem far lower than are now being observed in field studies (Bull and others 1997, Lundquist and Mariani 1991). The existing models have also focused just on snags and have provided only deterministic point values of snag sizes or densities and of population response (“population potential”) instead of probabilistic estimates more amenable to a risk analysis and risk management framework.

The existing models have focused on terrestrial vertebrate species that are primary cavity excavators. The assumption made by Thomas and others (1979) and Marcot (1992) is that secondary snag-using species would be fully provided for if needs of primary snag-excavating species were met. McComb and others (1992) and Schreiber (1987) indicate that secondary cavity nesting birds may be more sensitive to snag density than primary cavity excavators. The existing models also do not account for species that use different types of snags and partially dead trees, such as hollow live and dead trees used by bats (Betts 1998, Campbell and others 1996, Ormsbee and McComb 1998) and Vaux’s swift (Bull and Cooper 1990, Bull and Hohmann 1993). These new findings are important to improving dead wood models for wildlife.

A New Model: DecAID

Our goal for developing the DecAID model was to advise managers on the numbers, sizes, species, and decay classes of dead wood needed to help maintain wildlife habitat and ecosystem functions in forests. We intend for the model to provide such advice by wildlife habitat and management objective. In addition to snags and down logs, the advisory model will address diseased, partially dead, or decaying live trees, including hollow trees, as important wildlife habitat components. Whereas providing advice on maintaining wildlife habitat will be a main objective of the model, the model will be ecosystem-based and also provide information on ecosystem functions performed by wildlife associated with dead wood, maintenance of ecological function (e.g., soil productivity), roles of insects and diseases in the creation and dynamics of dead wood, and management of fire *(fig. 1).* The modeling process will also help identify gaps in knowledge of dead wood as wildlife habitat and its role in ecosystem processes.

User Inputs

Three pieces of information will be required as user inputs: wildlife habitat type, structure stage, and management objective *(fig. 1).* The first input, wildlife habitat type, is defined by the SHP (Johnson and O'Neil 2001). Examples include major vegetation alliances such as eastside mixed-conifer forest, southwest Oregon mixed-conifer/hardwood forest, and westside lowlands conifer/hardwood forest (Marcot and others 2002). The SHP describes 26 structural stages, which are combined into three successional stages for analysis of inventory data (Johnson and O'Neil 2001). The successional stages are early, mid-, and late-successional forests (Ohmann and Waddell 2002). For species use data we combined the mid- and late-successional stages into one class due to the way most data were reported in the literature. The management objective is based on the landowner's expectations for managing for ecosystem function and diversity. Management objectives relate to statistical tolerance levels for managing for species and functions based on empirical data on species-dead wood relations. High, moderate, and low statistical levels have been developed (Marcot and others 2002). High confidence level might be applicable where maintaining or restoring ecosystem functions is the objective: for example, late-successional reserves from the Northwest Forest Plan. Low confidence levels might apply where maintaining some wildlife habitat and some level of ecosystem function such as site productivity are desired, but timber harvest is the main objective.

Species-Dead Wood Relations

The wildlife or species component of DecAID focuses on species needs for sizes, amounts, and distribution of dead wood, primarily snags and down wood. We extensively reviewed the literature, contacted researchers, and summarized quantitative data on dead and decaying wood relationships of fungi, amphibians, birds, and mammals. We found many data gaps for some habitats and species groups. To make the model as complete as possible, we used unpublished data to fill in some of the gaps. We arranged the species use data into three cumulative species curves representing high, moderate, and low statistical levels for each combination of wildlife habitat type and structure stage for which data were available (Marcot and others 2002). Expert opinion was used to help interpret the data and species curves.

The DecAID output produces a list of wildlife species associated with dead wood and a list of ecological functions performed by those species *(fig. 1).* We queried data matrices developed by the SHP to develop the lists. One query links to a Habitat Features database that lists species associations with different types and amounts of dead and decaying wood, including snags, remnant trees (that possibly have some dead parts), mistletoe and witch's brooms, dead parts of live trees, hollow trees, tree cavities, bark crevices, down wood, litter, and duff. Lists of species associated with these elements can be linked to a Key Ecological Functions database to produce a list of functions the dead-wood-associated species perform in the ecosystem.

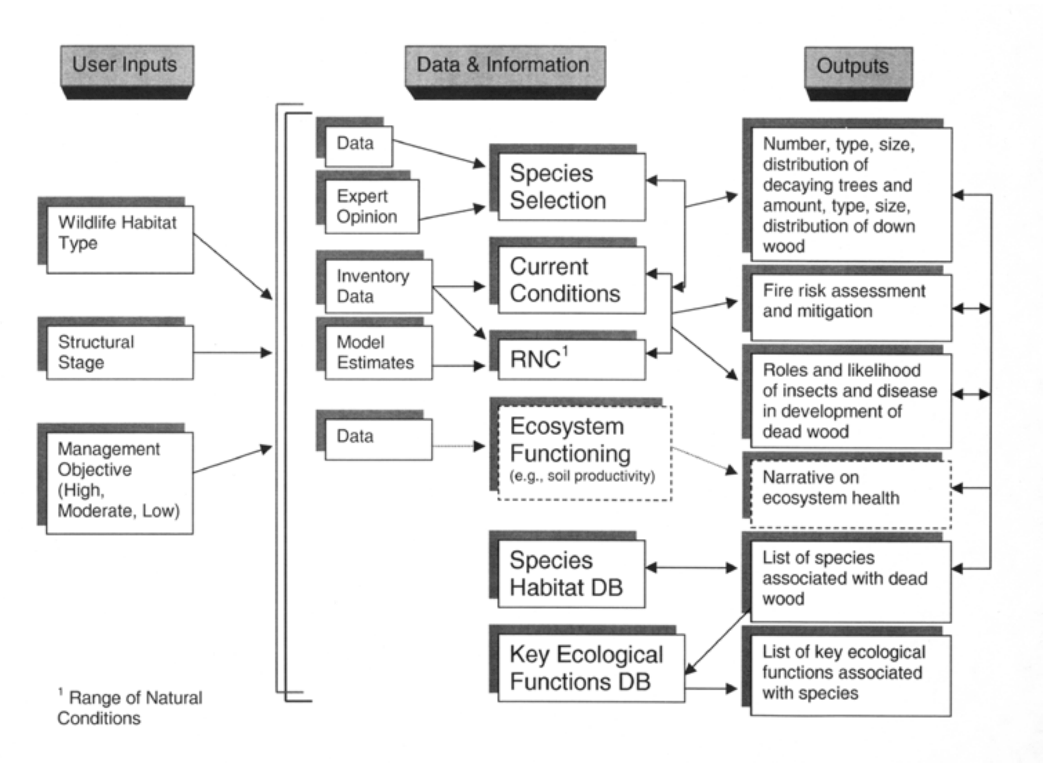

Figure 1—Flowchart of the DecAID model.

Inventory Data

We are using inventory data from nearly 17,000 Forest Service Continuous Vegetation Survey (CVS) and Forest Inventory and Analysis (FIA) plots, and USDI Bureau of Land Management Natural Resource Inventory (NRI) plots to estimate current amounts and condition of dead wood across private and public lands in Oregon and Washington (Ohmann and Waddell 2002). The data are stratified by wildlife habitat type and structure stage. Data from plots in reserved areas, which we assume to represent unharvested conditions, are used to estimate range of natural conditions (RNC) or historic levels of dead wood. This approach works better for wetter areas west of the Cascade crest where fire suppression has had less influence on dead wood resources than in drier habitats. In some Wildlife Habitat Types, especially east of the Cascade crest, a combination of fire suppression, insect outbreaks, salvage, and firewood cutting might limit our ability to determine natural levels of dead wood based on existing conditions. In these areas, models such as that of Harrod and others (1998) may provide more realistic benchmarks for natural levels of dead wood.

In DecAID, the information based on species' use of dead wood is compared to sizes and amounts of dead wood in unharvested stands. This comparison assists in determining if species are using dead wood at different levels than commonly occur in natural stands, and the potential of a stand to produce dead wood. The inventory data can also give us some ideas about distribution of dead wood in natural systems. We should also be able to show how well current conditions are meeting species needs and how closely current conditions reflect RNC.

Natural Processes

Insects and Diseases

The influence of insects and diseases (used here to include pathogenic and decay-causing fungi and dwarf mistletoes) on recruitment of dead wood through time is assessed in the model. We obtained occurrence and severity frequencies of plots or trees affected by selected insect and/or disease species from the inventory data for each wildlife habitat type and structure stage. This portion of the model provides a list of the insects and diseases that are most likely to generate dead or decaying wood in each habitat. DecAID will then provide generalized predictions about the future amounts and types of dead and decaying wood that may occur naturally in stands. Each type of insect or disease produces a different type of dead wood or decay that subsequently may provide a different function for dead-wood-associated species. This portion of the model also will provide advice on how to mitigate or intensify the activity of these agents to decrease or increase dead wood recruitment.

Fire

The fire portion of DecAID has not yet been developed. Our plan is to assess the fire likelihoods associated with the amount and distribution of dead wood indicated by species use data. Information will be provided to help the land manager balance the needs of species with the risk of catastrophic fire.

Ecosystem Function

Our intent for this portion of the model is to provide qualitative and, where available, quantitative information on ecosystem functions affected by decadent wood, such as soil productivity, moisture retention, and slope stability. At this point, the time and funding necessary to complete a thorough literature review for these data are not available. We plan to use the qualitative information to provide a narrative review of the importance of dead and decaying wood to ecosystem functions *(fig. 1).*

Summary

DecAID is a new decayed wood advisory model currently being developed. Displaying the relationship of dead and decaying wood to wildlife habitat and species is a major component of the model. DecAID also provides advice on dead and decaying wood as an important component of ecosystems and the relationship of dead and decaying wood to natural processes. Inventory data are used to compare species needs to current amounts of dead wood in managed and unharvested forests.

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Regional Patterns of Dead Wood in Forested Habitats of Oregon and Washington[1]

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Abstract

We describe regional patterns of variation in dead wood across 20 million ha of upland forests of all ownerships in Oregon and Washington, based on an analysis of data on snags and down wood collected on over 16,000 field plots. Current patterns of dead wood are highly variable and complex. The strongest differences were among nine habitats that reflect strong regional gradients in physical environment and ecosystem processes. Mean snag density was lowest in the drier habitats east of the Cascade crest and greatest at higher elevations, ranging from 0.8/ha to 37.2/ha. The mean volume of down wood ranged from 7.4 m^3/ha in western juniper woodland to 183.3 m^3/ha in westside conifer-hardwood forest. Differences in dead wood were more pronounced among habitats west of the Cascade crest. Dead wood abundance generally increased with successional development. Large snags were more than twice as dense within wilderness areas than outside wilderness, whereas large down wood was more abundant outside wilderness. Dead wood on plots was non-normally distributed and skewed to the right. Information on regional patterns of variation in dead wood is being incorporated into the DecAID model, which will help guide managers in considering dead wood and processes of decomposition in forest management. The regional summaries of dead wood also can be used to evaluate forest practice regulations and incentive programs for non-Federal lands, and to assess wildlife habitat suitability, ecosystem health, and carbon stores at state, regional, and national levels.

Introduction

Dead trees are important elements of productive and biologically diverse forests. Dead trees form major structural features with many ecological functions, including habitat for organisms, energy flow and nutrient cycling, and geomorphic processes (Harmon and others 1986). Yet, little is known about how amounts and characteristics of dead wood vary across broad regions that encompass a wide range of ecological conditions and disturbance histories.

Although the bulk of published data is from small-scale ecological plots, other forms of data exist but have not been analyzed. For example, resource inventories by Federal agencies include a wealth of information on snags (standing dead trees) and

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down wood (fallen trees) across the Pacific Northwest. This study describes current patterns of dead wood in Oregon and Washington by analyzing data collected on regional grids of field plots. In this paper we present a preliminary analysis of dead wood abundance in wildlife habitats of upland forests ("habitats"). We focused on 9 of the 31 major habitats that were developed for the Species Habitat Project (Chappell and others 2001). Our goal was to provide basic information about ecological patterns, as context for management decisions at stand, landscape, and ecoregion scales, and for analyzing forest policies at regional and national levels.

Study Area

The study area encompasses a region of temperate forest within the states of Washington and Oregon. The Cascade Range is the major topographic and climatic divide, and in this paper we refer to areas west of the Cascade crest as "westside" and east of the crest as "eastside." Elevations range from sea level to nearly 3,000 m. Vulcanism shaped much of the landscape, but sedimentary and metamorphic rocks are plentiful, and deposition of parent materials by alluvial, colluvial, and eolian processes is common. Soil types are primarily inceptisols, spodosols, and ultisols. The westside has a maritime climate with wet winters and dry summers, and the eastside climate is drier and more continental.

Forests cover 19.6 million ha in the study area, about half of which is publicly owned (Powell and others 1993). Forests are dominated by coniferous trees (Franklin and Dyrness 1988). Hardwoods tend to occupy harsh sites, riparian areas, or disturbed areas, except in southwest Oregon. The mesic temperate coniferous forests of northwestern Washington and Oregon contain the greatest biomass accumulation and highest productivity rates in the world (Waring and Franklin 1979). See Franklin and Dyrness (1988) and Ohmann and Spies (1998) for detailed descriptions of Washington and Oregon plant communities and environmental gradients.

Before European settlement, fire was the predominant natural disturbance (Agee 1993), but in the last 100 years timber management and wildfire suppression have altered forest succession. Even-aged forest management practices are most common in northwestern Oregon and Washington, whereas uneven-aged management predominates in southwestern Oregon and on the eastside. On the eastside, fire suppression has allowed fire-sensitive and late-successional tree species to increase in density, and selective harvests have influenced forest composition.

Source of Data and Sample Design

Data on dead wood have been collected from extensive grids of field plots as part of ongoing, strategic-level inventories conducted by the USDA Forest Service in the Pacific Northwest for many years, and more recently by the USDI Bureau of Land Management (BLM) *(table 1).* National, state, and county parks and privately owned reserves had not been surveyed at the time of this study. Because plots were installed throughout the study area in a systematic fashion, the diversity of forests found in both states was sampled.

Table 1—*Sources of data on live trees, snags, and down wood from regional forest inventories in Oregon and Washington.*

Inventory program	Ownerships sampled	Sample grid spacing[1]	Sample weight[2]	Inventory dates	Number of plots[3]
Forest Inventory and Analysis (FIA)	Non-Federal	5.5 km	1.0	1984-1991	[4]3,994
Current Vegetation Survey (CVS)	National Forest	2.7 km outside wilderness	0.25	1991-1995	11,958
		5.5 km inside wilderness	1.0	1991-1995	580
Natural Resource Inventory (NRI)	Bureau of Land Management in western Oregon	5.5 km	1.0	1997	335

[1] Plots on the 5.5-km grid represent about 3,000 ha; plots on the 2.7-km grid represent about 750 ha.

[2] Weight applied to plot-level dead wood data in computing descriptive statistics. For NRI and CVS plots with multiple condition classes, weights were reduced proportional to the area occupied.

[3] Includes only those plots on which dead wood data were collected. Does not include 319 plots in aspen, dunes, riparian, and wetland habitats.

[4] Down wood data collected only on 886 plots in eastern Washington. Snag data collected on all plots.

The inventories provided data on stand characteristics, live trees, snags, and down wood collected on 16,867 field plots from 1984-1997 on forest land across Oregon and Washington *(fig. 1)*. Field plots consisted of a cluster of up to five subplots and included a series of fixed- and variable-radius circular plots. The Forest Inventory and Analysis (FIA) plot was confined to a single, homogenous forest condition by moving subplots according to a predetermined pattern. In contrast, the Current Vegetation Survey (CVS) and Natural Resource Inventory (NRI) subplots were installed in fixed positions, and the plot could encompass multiple forest conditions. Live trees and snags were sampled on circular plots, and down wood was sampled along transect lines (DeVries 1973, Waddell 2002) established within plot boundaries. The species, diameter at breast height (DBH), and decay class (adapted from Cline and others 1980) were recorded for each snag tallied. Down wood measurements included the species, diameter at the point of intersection and at large end, piece length, decay class, and evidence of use by wildlife. Detailed information about inventory sample designs, field procedures, and compilation methods are available from the individual agencies that conducted the inventories (see also Max and others 1996, USDA Forest Service 1992, CVS Web site "www.fs.fed.us/r6/survey").

We assigned each plot to an ecoregion (U.S. Environmental Protection Agency 1995) by overlaying the plot locations on the ecoregion map in a geographic information system (GIS). We also obtained data from the agencies on the reserve status of each plot. Plots were coded as within areas set aside by Congress (Wilderness and Wild and Scenic Rivers), by agency administration or as unreserved.

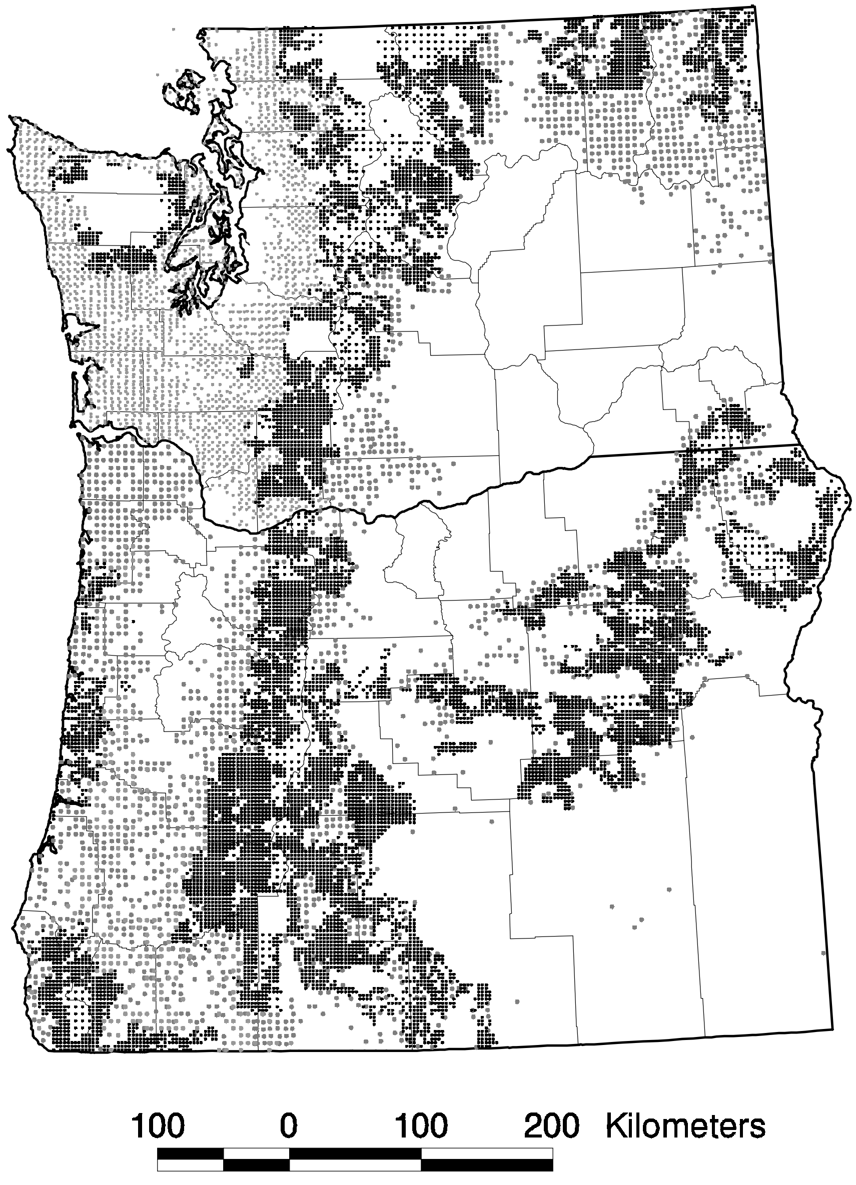

Figure 1—Locations of Natural Resources Inventory (NRI), Current Vegetation Survey (CVS), and Forest Inventory and Analysis (FIA) field plots used in this study, Oregon and Washington. Only those plots where dead wood data were collected are shown. Black symbols are plots on Federal lands (NRI and CVS); gray symbols are plots on non-Federal lands (FIA).

Data Compilation and Analysis

We compiled the source data from the three inventories into one database that contains data tables for stand-level attributes, live trees, snags, and down wood. This involved converting codes and measurement units, calculating new variables, and making other technical modifications to insure that all data were in a common format for regional analysis. We calculated new variables from the down wood data collected with the line intersect sampling method to produce per-hectare estimates of down wood density (number of pieces), volume, and percent cover for each inventory plot (DeVries 1973, Waddell 2002). We also calculated per-hectare estimates of snag density. We were not able to compute snag volume at the time of this writing because many snag heights were missing in the CVS and NRI data.

We evaluated the CVS and NRI plots for the presence of multiple forest conditions. If a plot encompassed more than one land class (forest or nonforest), or more than one vegetation series (defined by the tree species that would dominate the site in the absence of disturbance) within forest land, we identified separate condition-classes on the plot. The live and dead tree data were partitioned among the condition-classes accordingly. We treated these condition-class plots as independent observations in our analyses, and refer to them simply as “plots” in this paper.

Stand-level variables and live tree data were used to classify each plot into a wildlife habitat type (“habitat”), alliance group, and successional stage. We used the habitats and some of the alliances from the classification system defined by the Species Habitat Project (Chappell and others 2001). We developed classification algorithms that utilized the set of variables we had available in the inventory database. Habitat was determined by evaluating the potential vegetation (series) and ecoregion assigned to the plot, and alliance was determined by examining a combination of potential and current vegetation variables as follows (scientific names of tree species are listed in *appendix A):*

Habitat and alliance group	**Definition**
Westside conifer-hardwood type:	Western redcedar, Sitka spruce, western hemlock, grand fir, white fir, and Port-Orford cedar series in westside ecoregions.
Hardwood alliance	Hardwoods ≥70 pct and conifers <30 pct of stocking[1]
Conifer-hardwood mixed alliance	Hardwoods 31-69 pct and conifers 31-69 pct of stocking[1]
Conifer alliance	Hardwoods ≤30 pct and conifers ≥70 pct of stocking[1]; not a Sitka spruce site (see below).
Sitka spruce/western hemlock alliance	Hardwoods ≤30 pct and conifers ≥70 pct of stocking[1]; Sitka spruce series or Sitka spruce present.
Westside white oak-Douglas-fir type:	Douglas-fir or Oregon white oak series in westside ecoregions.
Douglas-fir alliance	Douglas-fir series outside southwest Oregon; Oregon white oak absent.
Douglas-fir/white oak alliance	Oregon white oak series or Oregon white oak present.
Southwest Oregon mixed conifer-hardwood type	Ponderosa pine, Douglas-fir, jeffrey pine, grand fir, white fir, Port-Orford cedar, tanoak, or canyon live oak series in southwest Oregon.

Habitat and alliance group	Definition
Montane mixed-conifer type	Engelmann spruce, noble fir, Shasta red fir, Pacific silver fir, subalpine fir, and mountain hemlock series.
Subalpine parkland type	Open parkland series of subalpine fir, mountain hemlock, subalpine larch, Alaska yellow-cedar, and whitebark pine.
Eastside mixed-conifer type	Douglas-fir, grand fir, white fir, western redcedar, western hemlock, and noble fir series in eastside ecoregions.
Lodgepole pine type	Lodgepole pine series in eastside ecoregions.
Eastside ponderosa pine type:	Ponderosa pine, Oregon white oak, and black oak series in eastside ecoregions.
Ponderosa pine/Douglas-fir alliance	Oregon white and black oak absent.
Ponderosa pine/white oak alliance	Oregon white or black oak present.
Western juniper type	Western juniper series.

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[1] Relative stocking of all live trees in the stand, *sensu* Maclean (1979).

The Species Habitat Project (Chappell and others 2001) identified 26 structural stages of forest vegetation that are important as wildlife habitat. Because this classification system was too complex for our region-wide analysis, we grouped the 26 structural stages into three successional stages that we assume to be correlated with stand age or time since major disturbance. The stages were defined by current vegetation structure as follows:

Successional Stage	Definition
Early	Tree stocking[1] < 10 percent, or tree stocking ≥10 percent and quadratic mean diameter[2] ranging from 2.5-24.9 cm.
Middle	Tree stocking ≥10 percent and quadratic mean diameter[2] ranging from 25.0-49.9 cm.
Late	Tree stocking >10 percent and quadratic mean diameter[2] ≥ 50.0 cm.

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[1] Relative stocking of all live trees in the stand on the plot, *sensu* Maclean (1979).

[2] The diameter of the tree of average cross-sectional area at breast height (1.37 m) on the plot.

We computed descriptive statistics for snags and down wood within habitats by weighting the plots according to the sampling grid intensity *(table 1)* and the proportion of the plot within the condition-class. We summarized the characteristics of snags and down wood only for habitats and successional stages sampled by at least 10 plots. Wetlands, coastal dunes, aspen, and riparian forests were not well represented in the inventory sample and were excluded from our analysis.

We evaluated differences in dead wood among habitats using analysis of variance for unbalanced designs, with observations (plots) weighted as described above, using generalized linear models in SAS (SAS Institute Inc. 1988). We compared successional stages within each habitat and alliance and compared habitats with all successional stages combined. Where overall *F* tests were significant (alpha

$\geq$ 0.05), we conducted multiple comparisons of means using the Tukey-Kramer method (SAS Institute Inc. 1988).

Because we used data collected from different sampling designs, a variety of tree tally criteria were applied in the field. Our snag and down wood analyses include trees of the following characteristics common to all datasets: snags $\geq$25.4 cm DBH and $\geq$2.0 m tall of decay classes 1-5; down wood $\geq$12.5 cm diameter at point of intersection and $\geq$2.0 m long of decay classes 1-5 (except decay classes 1-4 for FIA plots). We summarize dead wood for two groups: "total snags" or "total down wood," which includes snags $\geq$25.4 cm DBH or down wood $\geq$ 12.5 cm diameter at large end; and "large snags" or "large down wood," which includes snags $\geq$50 cm DBH or down wood $\geq$ 50 cm diameter at large end.

Results

Differences in Dead Wood Among Habitats and Alliances

We present snag results in terms of density *(tables 2-3),* and down wood in terms of volume *(tables 4-5),* cover *(tables 6-7),* and density *(tables 8-9).* We limit our discussion of down wood to volume, but patterns of cover and density were similar. All results represent weighted means of plot-level, per-hectare estimates for a category of interest.

The abundance of snags and down wood varied substantially across the region. The greatest differences in dead wood were among the habitats, although differences among successional stages within habitats also were significant in many cases. Total snag densities were greatest at higher elevations: 37.2/ha in montane mixed-conifer forest and 36.0/ha in subalpine parks *(table 2).* Snags were least dense in the drier habitats on the eastside: 0.8/ha in western juniper woodland and 5.0/ha in eastside ponderosa pine *(table 2).* Large snags were most abundant in montane mixed-conifer forest (9.6/ha) and in westside conifer-hardwood forest (5.5/ha), and least abundant in western juniper woodland (0.2/ha) and eastside ponderosa pine woodland (1.0/ha) *(table 3).* The volumes of both total and large down wood were greatest in westside conifer-hardwood forest and lowest in western juniper woodland *(table 4).* Total down wood volume among habitats ranged from 7.4 to 183.3 m^3/ha and large wood from 4.5 to 131.8 m^3/ha.

Pairwise differences in total dead wood generally were more pronounced among habitats west of the Cascades than among the eastside types. Differences between westside habitats (conifer-hardwood, white oak-Douglas-fir, southwest Oregon mixed conifer-hardwood) were always significant for both snags and down wood. The amounts of total snags and down wood in montane mixed-conifer forests were significantly different from almost all other habitats.

Successional Patterns of Dead Wood

Snag density generally increased with stand development. Within habitats and alliances, total snag density always was lowest in the early successional stage and usually was highest in the late stage *(table 2).* The abundance of large snags increased with successional development in all of the habitats and alliances except the hardwood alliance of westside conifer-hardwood forest and in western juniper woodland, where differences were not significant *(table 3).* Differences in snag density were significant between at least two successional stages in all of the habitats and alliances except the hardwood alliance of westside conifer-hardwood forest, the eastside ponderosa pine alliances, and western juniper woodland *(tables 2-3)*.

The volume of down wood also generally increased with forest development, but successional patterns differed somewhat among the habitats and alliances *(tables 4-5)*. Late successional stages contained the largest concentrations of both total and large down wood in most of the habitats and alliances *(tables 4-5)*. In the westside habitats and in montane mixed-conifer forest, down wood volume in the late stage usually was significantly different from the early and middle stages, but early and middle stages usually were not significantly different from one another *(tables 4-5)*. Large down wood volumes differed significantly between the early and middle successional stages in all of the eastside habitats and alliances except the ponderosa pine/white oak alliance and western juniper woodland *(table 5)*.

Table 2—*Weighted mean (standard error) density of "total" snags $\geq$25.4 cm DBH, decay classes 1-5, and $\geq$2 m tall by habitat, alliance, and successional stage, Oregon and Washington.*[1]

	Successional stage			
Habitat and alliance	**Early**	**Middle**	**Late**	**All stages**
	Mean (SE) trees per hectare			
Westside conifer-hardwood:				
Hardwood	5.6 (1.1)	13.3 (1.2)	9.3 (3.6)	11.0 (0.9)
Conifer-hardwood mixed	^{a}5.3 (0.8)	^{b}12.3 (0.9)	^{b}14.6 (1.9)	10.2 (0.6)
Conifer	^{a}5.2 (0.4)	^{b}21.4 (0.8)	^{c}34.0 (1.1)	16.1 (0.5)
Sitka spruce/western hemlock	^{a}4.3 (0.7)	^{b}16.1 (1.4)	^{b}27.8 (3.1)	12.4 (0.9)
All alliances	^{a}5.1 (0.3)	^{b}17.9 (0.6)	^{c}31.4 (1.0)	14.3 (0.3)
Westside white oak-Douglas-fir:				
Douglas-fir	6.5 (2.3)	12.2 (2.0)	20.7 (4.0)	11.6 (1.5)
Douglas-fir/white oak	^{a}6.1 (1.3)	^{a}10.6 (1.3)	^{b}14.5 (3.0)	9.3 (0.9)
All alliances	^{a}6.3 (1.1)	^{a}11.3 (1.1)	^{b}17.1 (2.5)	10.2 (0.8)
Southwest Oregon mixed conifer-hardwood	^{a}9.5 (1.1)	^{b}17.1 (0.9)	^{b}21.0 (1.0)	15.4 (0.6)
Montane mixed-conifer	^{a}17.8 (1.4)	^{b}49.3 (1.3)	^{c}40.3 (1.4)	37.2 (0.9)
Subalpine parkland	34.8 (7.4)	37.3 (4.3)	[2]NA	36.0 (4.3)
Eastside mixed-conifer	^{a}14.8 (0.9)	^{b}21.5 (0.6)	20.7 (1.6)	19.4 (0.5)
Lodgepole pine	^{a}16.5 (1.5)	^{b}27.6 (2.6)	[2]NA	19.8 (1.3)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	4.8 (0.5)	4.8 (0.4)	5.3 (0.8)	4.8 (0.3)
Ponderosa pine/white oak	7.1 (1.6)	7.5 (1.9)	[2]NA	7.1 (1.2)
All alliances	5.0 (0.4)	5.0 (0.4)	5.2 (0.8)	5.0 (0.3)
Western juniper	0.7 (0.2)	1.6 (0.4)	0.8 (0.5)	0.8 (0.2)
All habitats	^{a}9.1 (0.3)	^{b}21.3 (0.3)	^{c}28.4 (0.6)	17.4 (0.2)

[1] Significantly different means (alpha $\leq$ 0.05) within rows (among successional stages) are indicated by different letter footnotes.

[2] Not applicable—sample size <10 plots.

Table 3—*Weighted mean (standard error) density of "large" snags ≥50.0 cm DBH, decay classes 1-5, and ≥2 m tall by habitat, alliance, and successional stage, Oregon and Washington.*[1]

Habitat and alliance	Successional stage			
	Early	**Middle**	**Late**	**All stages**
	Mean (SE) trees per hectare			
Westside conifer-hardwood:				
Hardwood	2.6 (0.6)	3.5 (0.4)	2.0 (1.0)	3.2 (0.3)
Conifer-hardwood mixed	[a]2.1 (0.5)	[b]4.2 (0.3)	[b]7.8 (1.1)	3.7 (0.3)
Conifer	[a]2.1 (0.2)	[b]7.5 (0.4)	[c]15.6 (0.5)	6.4 (0.2)
Sitka spruce/western hemlock	[a]2.1 (0.3)	[b]5.3 (0.5)	[c]12.4 (1.4)	4.7 (0.3)
All alliances	[a]2.1 (0.1)	[b]6.0 (0.2)	[c]14.3 (0.5)	5.5 (0.2)
Westside white oak-Douglas-fir:				
Douglas-fir	2.5 (1.1)	3.3 (0.5)	7.6 (1.4)	3.5 (0.5)
Douglas-fir/white oak	[a]0.9 (0.2)	[b]2.0 (0.3)	[c]4.8 (1.0)	1.9 (0.2)
All alliances	[a]1.4 (0.4)	[a]2.6 (0.3)	[b]5.9 (0.9)	2.5 (0.2)
Southwest Oregon mixed conifer-hardwood	[a]2.6 (0.3)	[b]5.0 (0.3)	[c]9.5 (0.5)	5.1 (0.2)
Montane mixed-conifer	[a]3.0 (0.3)	[b]10.5 (0.4)	[c]21.7 (0.7)	9.6 (0.3)
Subalpine parkland	[a]1.7 (0.5)	[b]5.6 (1.0)	[2]NA	3.6 (0.6)
Eastside mixed-conifer	[a]2.1 (0.2)	[b]4.2 (0.1)	[c]8.0 (0.6)	3.8 (0.1)
Lodgepole pine	[a]0.8 (0.1)	[b]2.2 (0.3)	[2]NA	1.2 (0.1)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	0.9 (0.1)	0.9 (0.1)	1.4 (0.3)	0.9 (0.1)
Ponderosa pine/white oak	1.0 (0.4)	3.2 (1.0)	[2]NA	2.1 (0.6)
All alliances	0.9 (0.1)	1.1 (0.1)	1.4 (0.2)	1.0 (0.1)
Western juniper	0.1 (0.0)	0.5 (0.2)	0.1 (0.2)	0.2 (0.1)
All habitats	[a]2.0 (0.1)	[b]5.3 (0.1)	[c]13.3 (0.3)	4.9 (0.1)

[1] Significantly different means (alpha ≤ 0.05) within rows (among successional stages) are indicated by different letter footnotes.

[2] Not applicable—sample size <10 plots.

Table 4—*Weighted mean (standard error) volume of "total" down wood $\geq$12.5 cm large end diameter, decay classes 1-4, and $\geq$2.0 m long by habitat, alliance, and successional stage, Oregon and Washington.*[1]

	Successional stage			
Habitat and alliance	**Early**	**Middle**	**Late**	**All stages**
	Mean (SE) cubic meters per hectare			
Westside conifer-hardwood:				
Hardwood	67.0 (20.1)	142.0 (33.1)	[2]NA	125.0 (23.7)
Conifer-hardwood mixed	192.1 (31.6)	166.6 (24.7)	148.3 (39.1)	172.2 (17.4)
Conifer	[a]150.8 (8.2)	[a]168.4 (6.7)	[b]229.2 (9.0)	185.4 (4.7)
Sitka spruce/western hemlock	[a]123.6 (27.2)	173.2 (22.2)	[b]232.2 (29.8)	183.4 (15.8)
All alliances	[a]151.8 (7.6)	[a]167.7 (6.2)	[b]226.3 (8.4)	183.3 (4.3)
Westside white oak-Douglas-fir:				
Douglas-fir	82.8 (18.6)	57.7 (13.5)	88.8 (20.6)	70.7 (9.6)
Douglas-fir/white oak	26.4 (10.7)	36.3 (4.2)	57.0 (12.0)	37.8 (4.0)
All alliances	54.0 (11.7)	44.2 (6.1)	71.2 (12.3)	51.3 (5.1)
Southwest Oregon mixed conifer-hardwood	[a]84.9 (8.6)	[a]68.8 (4.6)	[b]118.6 (8.0)	85.9 (3.8)
Montane mixed-conifer	[a]102.1 (6.4)	[a]112.5 (3.3)	[b]198.5 (10.6)	123.8 (3.2)
Subalpine parkland	35.1 (7.3)	55.2 (10.4)	[2]NA	44.0 (6.3)
Eastside mixed-conifer	[a]47.0 (2.2)	[b]54.6 (1.3)	[b]58.8 (4.9)	52.7 (1.1)
Lodgepole pine	50.0 (2.5)	55.4 (4.2)	[2]NA	51.4 (2.2)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	[a]21.6 (1.4)	[b]27.8 (1.4)	20.2 (3.0)	25.1 (1.0)
Ponderosa pine/white oak	16.9 (6.7)	35.5 (9.7)	[2]NA	27.4 (6.3)
All alliances	[a]21.3 (1.3)	[b]28.4 (1.4)	19.7 (3.0)	25.3 (1.0)
Western juniper	7.5 (3.1)	7.3 (1.9)	7.5 (4.7)	7.4 (1.9)
All habitats	[a]70.0 (1.9)	[b]77.6 (1.3)	[c]161.4 (4.5)	87.8 (1.2)

[1] Significantly different means (alpha $\leq$ 0.05) within rows (among successional stages) are indicated by different letter footnotes.

[2] Not applicable—sample size <10 plots.

Table 5—*Weighted mean (standard error) volume of "large" down wood ≥50.0 cm large end diameter, decay classes 1-4, and ≥2.0 m long by habitat, alliance, and successional stage, Oregon and Washington.*[1]

	Successional stage			
Habitat and alliance	**Early**	**Middle**	**Late**	**All stages**
	Mean (SE) cubic meters per hectare			
Westside conifer-hardwood:				
Hardwood	43.8 (17.8)	109.1 (32.7)	[2] NA	95.5 (23.2)
Conifer-hardwood mixed	146.9 (29.3)	129.0 (23.0)	112.4 (39.2)	132.3 (16.4)
Conifer	[a]95.4 (7.3)	[a]118.6 (6.3)	[b]173.9 (8.5)	132.3 (4.4)
Sitka spruce/western hemlock	[a]79.6 (25.7)	129.1 (21.6)	[b]180.8 (27.4)	136.6 (14.9)
All alliances	[a]98.5 (6.8)	[a]119.6 (5.7)	[b]172.1 (8.0)	131.8 (4.0)
Westside white oak-Douglas-fir:				
Douglas-fir	47.5 (17.2)	37.8 (12.1)	48.8 (18.1)	42.6 (8.6)
Douglas-fir/white oak	15.0 (8.6)	19.3 (4.0)	37.6 (11.1)	21.6 (3.6)
All alliances	30.9 (10.3)	26.1 (5.5)	42.6 (10.8)	30.2 (4.5)
Southwest Oregon mixed conifer-hardwood	[a]53.6 (7.5)	[a]42.6 (4.0)	[b]83.8 (7.4)	56.2 (3.4)
Montane mixed-conifer	[a]48.9 (5.6)	[a]46.2 (2.4)	[b]144.9 (9.6)	63.4 (2.8)
Subalpine parkland	7.3 (3.3)	22.3 (6.4)	[2] NA	14.5 (3.8)
Eastside mixed-conifer	[a]17.3 (1.8)	[b]23.0 (1.0)	[c]35.9 (4.2)	22.2 (0.9)
Lodgepole pine	[a]5.6 (0.9)	[b]14.6 (2.8)	[2] NA	8.1 (1.0)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	[a]10.4 (1.1)	[b]15.1 (1.2)	11.6 (2.4)	13.2 (0.8)
Ponderosa pine/white oak	8.7 (5.3)	20.3 (7.6)	[2] NA	15.2 (4.9)
All alliances	[a]10.3 (1.1)	[b]15.5 (1.2)	11.2 (2.4)	13.4 (0.8)
Western juniper	5.0 (2.8)	3.5 (1.6)	6.2 (4.6)	4.5 (1.7)
All habitats	[a]34.7 (1.6)	[b]40.5 (1.1)	[c]118.6 (4.1)	50.4 (1.0)

[1] Significantly different means (alpha ≤ 0.05) within rows (among successional stages) are indicated by different letter footnotes.

[2] Not applicable—sample size <10 plots.

Table 6—*Weighted mean (standard error) percent cover of "total" down wood* $\geq$*12.5 cm large end diameter, decay classes 1-4, and* $\geq$*2.0 m long by habitat, alliance, and successional stage, Oregon and Washington.*[1]

	Successional stage			
Habitat and alliance	**Early**	**Middle**	**Late**	**All stages**
	Mean (SE) percent cover			
Westside conifer-hardwood:				
Hardwood	2.1 (0.5)	3.4 (0.5)	[2]NA	3.1 (0.4)
Conifer-hardwood mixed	4.4 (0.6)	4.1 (0.5)	3.5 (0.6)	4.1 (0.3)
Conifer	[a]4.5 (0.2)	[a]4.6 (0.1)	[b]5.6 (0.2)	4.9 (0.1)
Sitka spruce/western hemlock	[a]3.5 (0.5)	4.7 (0.4)	[b]5.6 (0.6)	4.8 (0.3)
All alliances	[a]4.4 (0.2)	[a]4.5 (0.1)	[b]5.5 (0.2)	4.8 (0.1)
Westside white oak-Douglas-fir:				
Douglas-fir	2.7 (0.4)	1.7 (0.3)	2.6 (0.5)	2.2 (0.2)
Douglas-fir/white oak	[a]1.0 (0.3)	1.4 (0.1)	[b]1.8 (0.3)	1.4 (0.1)
All alliances	1.8 (0.3)	1.5 (0.1)	2.2 (0.3)	1.7 (0.1)
Southwest Oregon mixed conifer-hardwood	[a]2.5 (0.2)	[a]2.2 (0.1)	[b]3.2 (0.2)	2.5 (0.1)
Montane mixed-conifer	[a]3.8 (0.2)	[b]4.3 (0.1)	[c]5.1 (0.2)	4.3 (0.1)
Subalpine parkland	1.6 (0.3)	2.1 (0.4)	[2]NA	1.8 (0.2)
Eastside mixed-conifer	2.0 (0.1)	[a]2.2 (0.0)	[b]1.9 (0.1)	2.1 (0.0)
Lodgepole pine	2.9 (0.1)	2.8 (0.2)	[2]NA	2.9 (0.1)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	[a]0.9 (0.0)	[b]1.0 (0.0)	[a]0.7 (0.1)	0.9 (0.0)
Ponderosa pine/white oak	0.7 (0.2)	1.2 (0.3)	[2]NA	1.0 (0.2)
All alliances	[a]0.8 (0.0)	[b]1.0 (0.0)	[a]0.7 (0.1)	0.9 (0.0)
Western juniper	0.2 (0.1)	0.3 (0.1)	0.3 (0.2)	0.2 (0.0)
All habitats	[a]2.6 (0.1)	[b]2.7 (0.0)	[c]4.1 (0.1)	2.9 (0.0)

[1] Significantly different means (alpha $\leq$ 0.05) within rows (among successional stages) are indicated by different letter footnotes.

[2] Not applicable—sample size <10 plots.

Table 7—*Weighted mean (standard error) percent cover of "large" down wood $\geq$50.0 cm large end diameter, decay classes 1-4, and $\geq$2.0 m long by habitat, alliance, and successional stage, Oregon and Washington.*

	Successional stage			
Habitat and alliance	**Early**	**Middle**	**Late**	**All stages**
	Mean (SE) percent cover			
Westside conifer-hardwood:				
Hardwood	0.9 (0.3)	1.8 (0.5)	[2] NA	1.7 (0.4)
Conifer-hardwood mixed	2.5 (0.4)	2.2 (0.4)	1.8 (0.5)	2.2 (0.3)
Conifer alliance	[a]1.8 (0.1)	[a]2.2 (0.1)	[b]3.1 (0.1)	2.4 (0.1)
Sitka spruce/western hemlock	[a]1.3 (0.3)	2.6 (0.4)	[b]3.2 (0.4)	2.5 (0.2)
All alliances	[a]1.9 (0.1)	[a]2.2 (0.1)	[b]3.1 (0.1)	2.4 (0.1)
Westside white oak-Douglas-fir:				
Douglas-fir	0.9 (0.3)	0.8 (0.2)	0.9 (0.3)	0.8 (0.1)
Douglas-fir/white oak	0.3 (0.2)	0.5 (0.1)	0.8 (0.2)	0.5 (0.1)
All alliances	0.6 (0.2)	0.6 (0.1)	0.9 (0.2)	0.6 (0.1)
Southwest Oregon mixed conifer-hardwood	[a]0.9 (0.1)	[a]0.9 (0.1)	[b]1.6 (0.1)	1.1 (0.1)
Montane mixed-conifer	[a]1.0 (0.1)	[a]1.0 (0.0)	[b]2.9 (0.2)	1.3 (0.1)
Subalpine parkland	0.2 (0.1)	0.5 (0.1)	[2] NA	0.4 (0.1)
Eastside mixed-conifer	[a]0.4 (0.0)	[b]0.5 (0.0)	[c]0.7 (0.1)	0.5 (0.0)
Lodgepole pine	[a]0.2 (0.0)	[b]0.3 (0.1)	[2] NA	0.2 (0.0)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	[a]0.2 (0.0)	[b]0.3 (0.0)	0.3 (0.1)	0.3 (0.0)
Ponderosa pine/white oak	0.2 (0.1)	0.4 (0.2)	[2] NA	0.3 (0.1)
All alliances	[a]0.2 (0.0)	[b]0.3 (0.0)	0.3 (0.1)	0.3 (0.0)
Western juniper	0.1 (0.0)	0.1 (0.0)	0.2 (0.2)	0.1 (0.0)
All habitats	[a]0.7 (0.0)	[b]0.8 (0.0)	[c]2.2 (0.1)	1.0 (0.0)

[1] Significantly different means (alpha $\leq$ 0.05) within rows (among successional stages) are indicated by different letter footnotes.
[2] Not applicable—sample size <10 plots.

Table 8—*Weighted mean (standard error) density of "total" down wood ≥12.5 cm large end diameter, decay classes 1-4, and ≥2.0 m long by habitat, alliance, and successional stage, Oregon and Washington.*

	Successional stage			
Habitat and alliance	**Early**	**Middle**	**Late**	**All stages**
	Mean (SE) pieces per hectare			
Westside conifer-hardwood:				
Hardwood	199.4 (43.2)	193.0 (36.3)	[2] NA	185.9 (26.5)
Conifer-hardwood mixed	277.5 (39.0)	234.6 (22.2)	152.2 (29.5)	233.5 (18.1)
Conifer	[a]338.6 (15.7)	[a]255.4 (7.5)	[b]252.9 (7.2)	274.5 (5.5)
Sitka spruce/western hemlock	[a]244.8 (40.4)	281.4 (24.3)	[b]276.2 (34.4)	271.3 (18.5)
All alliances	[a]326.5 (13.9)	[a]254.3 (6.8)	[b]250.8 (7.0)	271.0 (5.1)
Westside white oak-Douglas-fir:				
Douglas-fir	220.8 (34.4)	104.8 (15.9)	140.1 (25.6)	136.7 (13.6)
Douglas-fir/white oak	[a]87.9 (37.9)	97.1 (11.4)	[b]107.0 (19.7)	97.6 (10.4)
All alliances	174.1 (27.4)	101.5 (10.2)	128.2 (18.5)	120.8 (9.3)
Southwest Oregon mixed conifer-hardwood	[a]158.9 (14.5)	[a]147.4 (7.8)	[b]172.3 (9.4)	157.0 (5.7)
Montane mixed-conifer	[a]254.1 (10.1)	[b]250.3 (6.5)	[c]222.3 (9.3)	246.7 (4.8)
Subalpine parkland	113.1 (17.2)	129.0 (19.4)	[2] NA	118.2 (12.5)
Eastside mixed-conifer	158.0 (4.9)	[a]142.9 (2.7)	[b]102.2 (6.6)	144.5 (2.3)
Lodgepole pine	201.6 (8.5)	161.2 (12.3)	[2] NA	190.9 (7.0)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	[a]71.1 (4.0)	[b]77.5 (3.0)	[a]43.7 (6.9)	73.0 (2.3)
Ponderosa pine/white oak	57.4 (23.9)	94.4 (16.9)	[2] NA	80.2 (13.5)
All alliances	[a]70.1 (3.9)	[b]78.8 (3.0)	[a]44.8 (6.8)	73.5 (2.3)
Western juniper	16.4 (4.3)	23.1 (6.1)	26.9 (16.4)	19.2 (3.4)
All habitats	[a]182.9 (3.5)	[b]167.2 (2.1)	[c]191.4 (4.0)	175.5 (1.7)

[1] Significantly different means (alpha ≤ 0.05) within rows (among successional stages) are indicated by different letter footnotes.

[2] Not applicable—sample size <10 plots.

Table 9—*Weighted mean (standard error) density of "large" down wood $\geq$50.0 cm large end diameter, decay classes 1-4, and $\geq$2.0 m long by habitat, alliance, and successional stage, Oregon and Washington.*

	Successional stage			
Habitat and alliance	**Early**	**Middle**	**Late**	**All stages**
	Mean (SE) pieces per hectare			
Westside conifer-hardwood:				
Hardwood	33.4 (12.6)	52.8 (17.1)	[2] NA	45.7 (11.1)
Conifer-hardwood mixed	71.8 (11.2)	48.1 (9.9)	32.2 (7.6)	53.4 (6.1)
Conifer	[a]60.0 (4.5)	[a]47.4 (2.5)	[b]59.7 (2.8)	54.8 (1.8)
Sitka spruce/western hemlock	[a]32.3 (9.4)	67.9 (11.5)	[b]72.7 (11.9)	62.0 (6.8)
All alliances	[a]59.0 (4.0)	[a]48.7 (2.3)	[b]59.6 (2.7)	55.0 (1.7)
Westside white oak-Douglas-fir:				
Douglas-fir	32.9 (8.3)	14.4 (4.2)	19.6 (6.2)	19.4 (3.3)
Douglas-fir/white oak	2.3 (3.3)	15.0 (2.8)	9.4 (4.9)	11.9 (2.1)
All alliances	22.2 (6.0)	14.6 (2.7)	16.0 (4.5)	16.3 (2.2)
Southwest Oregon mixed conifer-hardwood	[a]19.6 (2.9)	[a]18.3 (2.1)	[b]29.6 (3.0)	21.9 (1.5)
Montane mixed-conifer	[a]25.4 (2.3)	[a]21.5 (1.1)	[b]57.8 (3.6)	28.6 (1.1)
Subalpine parkland	6.5 (3.0)	10.9 (3.4)	[2] NA	8.5 (2.2)
Eastside mixed-conifer	[a]8.9 (0.6)	[b]10.5 (0.4)	[c]15.7 (1.7)	10.4 (0.3)
Lodgepole pine	[a]4.2 (0.7)	[b]7.9 (1.7)	[2] NA	5.3 (0.7)
Eastside ponderosa pine:				
Ponderosa pine/Douglas-fir	[a]5.8 (0.6)	[b]7.1 (0.6)	6.4 (1.5)	6.6 (0.4)
Ponderosa pine/white oak	6.3 (5.5)	8.8 (3.0)	[2] NA	7.6 (2.7)
All alliances	[a]5.8 (0.6)	[b]7.2 (0.5)	6.2 (1.4)	6.6 (0.4)
Western juniper	1.0 (0.5)	1.9 (1.0)	11.0 (8.2)	1.8 (0.6)
All habitats	[a]17.5 (0.8)	[b]17.1 (0.4)	[c]43.2 (1.4)	21.0 (0.4)

[1] Significantly different means (alpha $\leq$ 0.05) within rows (among successional stages) are indicated by different letter footnotes.

[2] Not applicable—sample size <10 plots.

Dead Wood in Wilderness Areas

Our analysis indicated that over all habitats, large snags were more than twice as dense in Federal wilderness areas than outside wilderness *(fig. 2A).* The strongest differences were for westside conifer-hardwood forest (5.1/ha outside wilderness vs. 15.2/ha inside wilderness), eastside mixed-conifer forest (3.2/ha vs. 9.5/ha), and lodgepole pine (0.8/ha vs. 3.4/ha). In contrast, large down wood was more abundant outside wilderness areas than in wilderness in all of the habitats *(fig. 2B),* although the differences often were not significant. The most pronounced differences in down wood volume were for southwest Oregon mixed conifer-hardwood (64.3 m^3/ha outside wilderness vs. 22.6 m^3/ha inside wilderness) and montane mixed-conifer (74.3 m^3/ha vs. 35.2 m^3/ha).

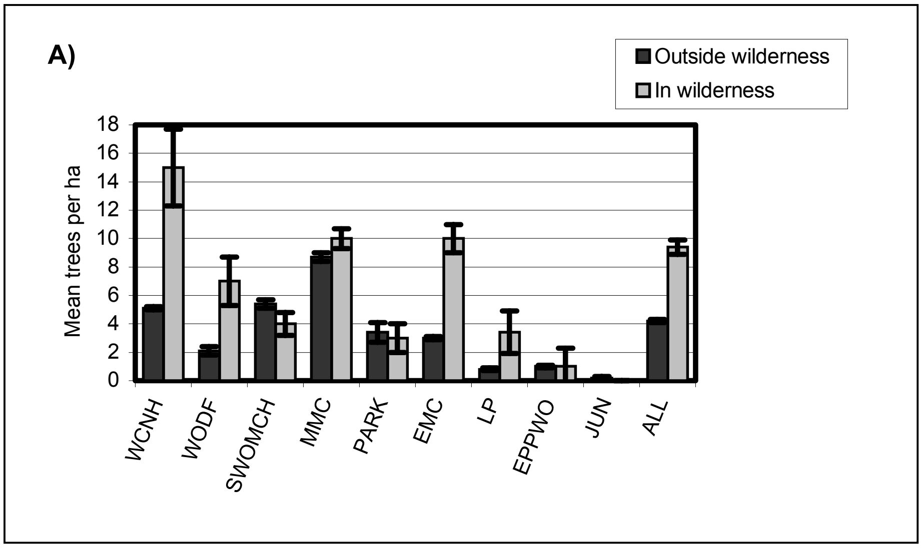
About 6.5 percent of the total area sampled for dead wood was in federally designated wilderness areas. The higher elevation habitats were best represented: 57 percent of the sampled area in subalpine park and 32 percent of montane mixed-conifer forest was in wilderness. Most poorly represented were western juniper woodland, eastside ponderosa pine, and westside conifer-hardwood forest (1.0, 0.3, and 1.5 percent of the sampled area, respectively).

Discussion

Causes of Regional Variability in Dead Wood Abundance

The regional differences in dead wood abundance among wildlife habitats reflect strong underlying gradients in physical environment and biological processes that affect community composition and structure, forest dynamics, and rates of dead wood input and decomposition. The amount and characteristics of dead wood in an ecosystem represent a balance between additions through tree death, breakage, and transport, and losses through processes of decomposition and fire consumption (Harmon and others 1986). The factors that influence these processes, and thus the spatial and temporal patterns of dead wood, are scale-dependent and incredibly complex. Our intent in this analysis was to present preliminary regional summaries of dead wood within vegetation types that describe distinct wildlife habitats in upland forests. (An in-depth analysis of factors that explain these patterns is beyond the scope of this paper.)

Westside conifer-hardwood forests have the highest net primary productivity of the habitats (Franklin 1988). Forest stands with greater density of live trees can be expected to have greater amounts of dead trees as well, and the high amount of dead wood we observed in the westside conifer-hardwood habitat probably can be explained by high rates of input within these productive forests. Rates of dead wood input also are influenced by rates of live tree mortality, which can increase as tree density surpasses that of a fully stocked stand. The large amount of dead wood in montane mixed-conifer forest may be explained in part by slow rates of decomposition in the cold temperatures at high elevations. The higher density of snags in the subalpine parkland and montane mixed-conifer types may be attributed to high mortality and low fall rates in these wildlife habitats. Unfortunately, published information on regional variation in rates of mortality, dead wood input, and decomposition, which would be very useful in interpreting our regional patterns of dead wood abundance, is scanty. A summary of existing studies in Washington and Oregon (Harmon and others 1986) showed greater input rates of dead wood biomass in mature and old-growth Douglas-fir and Sitka spruce/western hemlock forests (0.5-30 mg/ha/yr) than in higher elevation Pacific silver fir (0.3 mg/ha/yr), but data were not available for eastside forests.



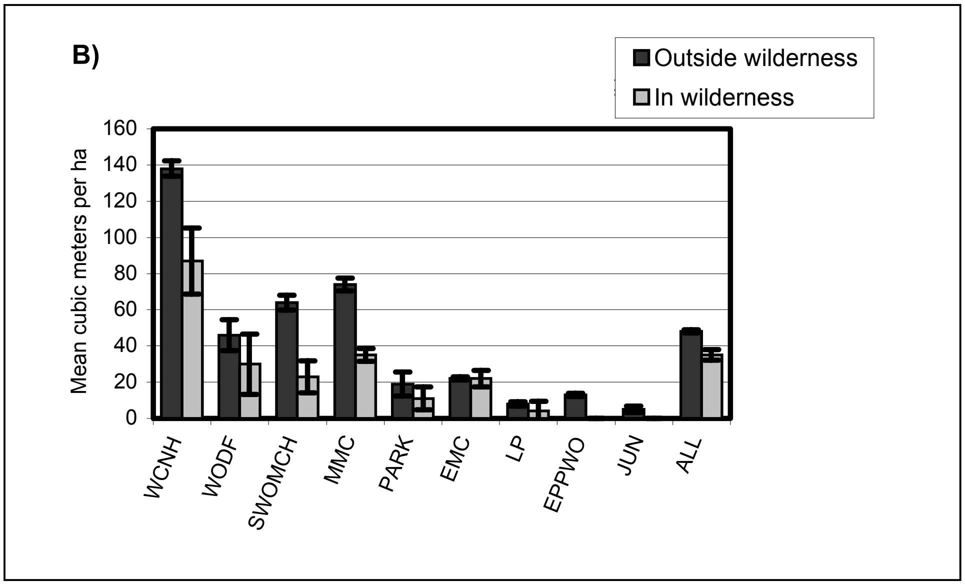


Figure 2—Abundance of dead wood by habitat and wilderness status, Oregon and Washington: A) is the weighted mean density of snags ≥50.0 cm DBH, decay classes 1-5, and ≥2 m tall; B) is the weighted mean volume of down wood ≥50.0 cm diameter at the large end, decay classes 1-4, and ≥2 m long. Error bars indicate one standard error of the mean. WCNH = westside conifer-hardwood, WODF = white oak-Douglas-fir, SWOMCH = southwest Oregon mixed conifer-hardwood, MMC = montane mixed-conifer, PARK = subalpine parkland, EMC = eastside mixed-conifer, LP = lodgepole pine, EPPWO = eastside ponderosa pine-white oak, JUN = western juniper, ALL = all wildlife habitats. There were <10 plots in western juniper in wilderness.

Current dead wood on a site also is influenced by disturbance and development of the current stand, and by the amounts of wood inherited from the preceding stand. Unfortunately, consistent information on the history of natural and human disturbance to the plots was not available for our analysis. Nevertheless, the successional stages used in our study represent distinct structural conditions that are surrogates for a chronosequence of stand development after stand-replacing disturbance. Although rate of biomass input and average piece size generally are thought to increase with succession (Harmon and others 1986), the amount of dead wood can follow a U-shaped pattern if young forests inherit large amounts of dead wood and live trees from preceding stands (Spies and others 1988). The snags in our study—especially large snags—increased with succession in almost all of the habitats. No wildlife habitats exhibited a U-shaped pattern, probably because snags tend to be cut within harvest units, which reduces the density found in early successional forests. Down wood also most often increased with succession, but this pattern was less consistent than for snags, and some habitats did exhibit a U-shaped pattern. Because we lacked data on the disturbance history of the plots and on the origin of individual pieces (from the current or a preceding stand), we can only speculate on why the habitats differed in this regard.

The lack of a U-shaped successional pattern for snags is not surprising. Snags have much shorter lag times in the forest than down wood: natural processes of fragmentation and decomposition begin much sooner, and they disappear as recognizable structures much faster (Harmon and others 1986). In addition, much of the dead wood in westside forests is input directly as down wood rather than snags (Harmon and others 1986). Snags also are much more likely than down wood to be damaged or intentionally removed by humans through the course of forest management and harvest activities. In an analysis of a subset of the same FIA data we used in this study (40- to 200-year-old stands on non-Federal lands in northwestern Oregon), Hansen and others (1991) found that large snags (>50.8 cm DBH) were three to five times as dense in stands that had never been clearcut than in stands that had been clearcut at least once. These factors taken together suggest that snag levels would more closely track recent disturbance and forest succession, while down wood amounts would be more strongly influenced by the long-term history and productivity of the site.

Information on the reserve status of the plots was our only available means for identifying forests unlikely to have been disturbed by timber harvesting and management. However, our comparisons of dead wood within and outside of wilderness areas must be interpreted with caution. Perhaps most importantly, the plots in wilderness do not sample complete environmental gradients—they are strongly biased towards higher elevations and lower productivities. We suspect these inherent productivity differences explain much of the higher amounts of down wood outside wilderness. On the other hand, if snags are more strongly influenced (i.e., reduced) by timber management activities than down wood as we suspect, then wilderness areas would be more likely to contain greater amounts of snags than areas outside wilderness—which is indeed what our data showed. In fact, Occupational Health and Safety Administration (OSHA) standards require the removal of most snags from harvest units for worker safety. Therefore, we would expect to find fewer snags in managed stands outside wilderness. If snags are cut and left on site, this would contribute to the larger amount of down wood we observed outside wilderness areas. In addition, high snag densities in higher elevation wildlife habitats (subalpine parkland and montane mixed conifer) could be the result of these areas being less accessible and less likely to be harvested for timber or firewood, regardless of their reserve status. Although wilderness areas are off-limits to future timber harvesting, they have been affected by other human activities to some degree (e.g., fire suppression, roads, recreation, exotic species introduction). Furthermore, many plots outside wilderness areas sample old-growth and younger forest on sites that have never been harvested.

Comparisons with Other Studies

Very few estimates of dead wood abundance at broad geographic scales are available for comparison with our numbers. Indeed, the lack of this kind of information was the primary motivation for this study. Direct comparisons are extremely difficult to make because of differences among studies in geographic location; the vegetation types, stand ages, and disturbance histories sampled; sampling design; definitions (e.g., dead wood sizes and decay classes); and units of measure (numbers of trees, volume, density, cover, or linear meters). Furthermore, this information often is not provided in the publications. Other regional studies of dead wood in Washington and Oregon have been restricted either to Federal or to nonfederal lands, which usually represent very different ecological conditions (Ohmann and Spies 1998). The study by Ohmann and others (1994) was limited to snags on non-Federal lands (a subset of the FIA data used in this paper), because data were unavailable for dead wood on Federal lands and down wood on non-Federal lands at that time. The study by Spies and others (1988) was confined to natural Douglas-fir forests > 40 years old on Federal lands on the westside. Published information for eastside forests is not available (Everett and others 1999), or consists of summaries of a few local studies (Bull and others 1997). Scientists for the Interior Columbia River Basin Ecosystem Management Project relied on expert opinion and local studies to estimate current and historical amounts of dead wood (Korol and others 2002). Harmon and others (1986) did not include any studies from eastern Washington or eastern Oregon.

Our large snag densities in westside conifer-hardwood forest *(table 3)* were substantially less than those reported by Spies and others (1988): our estimate of 2.1 large snags/ha in early stages probably represent stands younger than the 40 yr minimum sampled by Spies and others (1988); our estimate for middle-successinal stages of 6.0/ha compares to 27/ha in their young stands; and our estimate for late stages of 14.3/ha compares to their mature (16/ha) and old-growth (27/ha) classes.

On first inspection our estimates of down wood volume appear somewhat lower than other published numbers, but direct comparisons are not possible for reasons cited above. Although our estimates of mean down wood volume in successional stages of westside conifer-hardwood forest ranged from 151.8 to 226.3 m^3/ha *(table 4),* our maximum value on a plot was 2,142.9 m^3/ha. This compares to a range of 309 to 1,421 m^3/ha in various studies in westside Douglas-fir-western hemlock summarized by Harmon and others (1986) *(table 4),* and to 148 to 313 m^3/ha reported by Spies and others (1988).

We expect our estimates of down wood to be lower than other published studies for several reasons: our minimum diameter of 12.5 cm was slightly larger than the 10 cm minimum found in many other studies, which would reduce the number of down logs in the sample; we included managed as well as natural forests of all ages, not just older natural forests originating after fire; we excluded down wood of decay class 5; and our numbers are means across many stands, including stands where no down wood was observed (e.g., zero-tally plots), and maximum values are not presented. Our estimates of percent cover of down wood also may be lower than in other studies that used plot sampling or total tallies, as percent cover calculated from line intersect sampling has been shown to underestimate true values (Bate and others 1999).

Our dead wood estimates are not directly comparable to those reported in most wildlife studies (Marcot and others 2002). These studies typically are conducted within a local area and describe dead wood around nest sites, where it may be substantially higher than in surrounding stands because many wildlife species select nest sites within clumps of snags (Marcot and others 2002). Limited evidence suggests that dead wood is most often distributed randomly within stands, but sometimes is clumped (Cline and others 1980, Lutes 1999). Cline and others (1980) found that 25 percent of stands sampled in the Oregon Coast Range contained patches of 5-10 trees that died simultaneously.

Spatial Distribution of Dead Wood Abundance

In this paper we present regional-scale means of dead wood within wildlife habitats. The standard errors of these estimates are fairly low because of our very large sample sizes for most of the habitats and successional stages. In reality, the plot-level amounts of dead wood within the habitats were extremely variable. This variability reflects the high spatial and temporal variability in the many interacting environmental and disturbance factors that influence dead wood on a site. All of the habitats we examined had similar patterns: distributions were non-normally distributed and strongly skewed to the right. A large proportion of the plots did not contain snags or down wood, and a very small proportion of the plots contained extremely large accumulations of dead wood. Mean values for these skewed distributions must be interpreted with caution. We present the distributions of snags for the conifer alliance of westside conifer-hardwood forest to illustrate this pattern *(fig. 3)*. In this habitat, 39 percent of the area sampled had no snags, although the percentage of "zero" values is a function of the interaction between plot size and the spatial pattern of dead wood. Although plots contained a mean of 16 snags/ha, we observed densities as high as 215/ha.

Strengths and Limitations of the Inventory Data for Describing Dead Wood

The summaries of dead wood abundance we present in this paper represent the most extensive information of this kind yet available for Washington and Oregon. Valid comparisons among the habitats, alliances, and successional stages were possible because the data were derived from systematic grids of field plots, sample designs were similar among the datasets, and we applied consistent definitions in our analysis. The rigorous sample designs of the regional forest inventories allow calculation of unbiased estimates of known confidence for many characteristics of dead wood populations. However, because the grid design of the sample size is proportional to the vegetation type's occurrence in the landscape, uncommon habitats that may be of particular interest (such as streamside forests) are not represented in our study. In addition, some parts of the region were not sampled (down wood on non-Federal lands in Oregon and western Washington, and in national and state parks), and wilderness areas within National Forests were sampled at one quarter the intensity as areas outside wilderness.

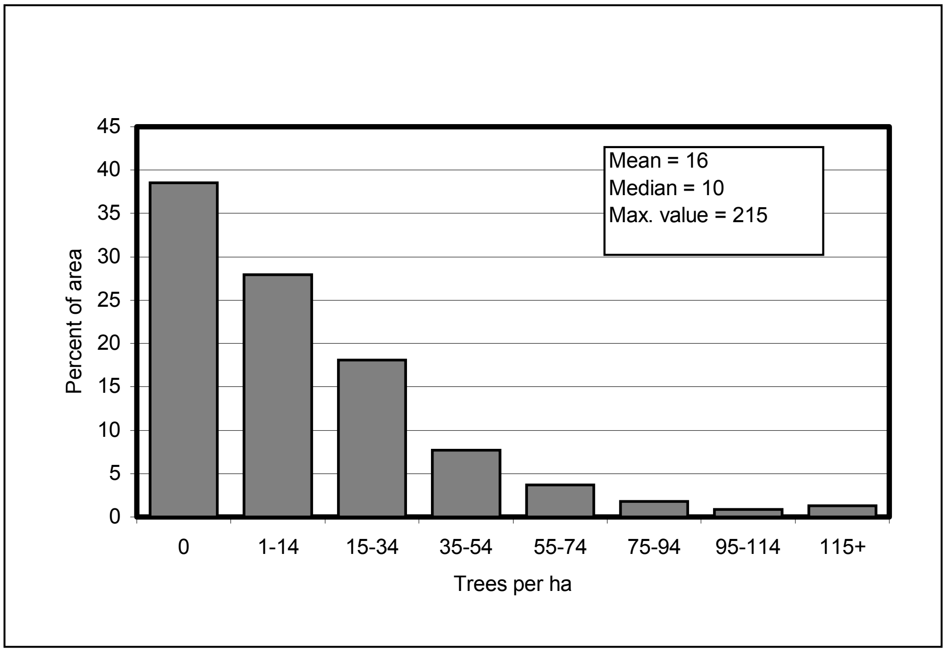


Figure 3—Density of snags ≥25.4 cm DBH, decay classes 1-5, and ≥2 m tall across plots in the conifer alliance of westside conifer-hardwood forest, Oregon and Washington, displayed as a percent of the sampled area.

The estimates of dead wood must be interpreted in light of the inherent scale imposed by the sample design. Our estimates describe the mean and variability of dead wood within vegetation types wherever they occur across Oregon and Washington, as sampled on field plots of a fixed, predetermined configuration. An individual plot samples an area that is smaller than a typical forest stand, and thus by itself does not provide an accurate estimate of stand-level conditions. Neither do we represent within-plot variability in this study. Information on stumps also is lacking from the forest inventory data. Stumps can serve as wildlife habitat as well as an indicator of the belowground system.

Although the estimates of amounts of dead wood are from plots measured at a single point in time, the current conditions express events that have occurred over the past decades to centuries. The most important limitation of our analysis was our inability—based on inventory data currently available—to investigate the effects of past disturbance on current amounts of dead wood. In particular, we were unable to compare dead wood in managed and unmanaged forests as defined in this study. The classification of the reserve status of the plots provides an imperfect stratification of disturbance history, as discussed earlier. Stand age has not been determined for plots on federal lands, and information on past harvesting and silvicultural activities is available only in narrative form for plots in National Forests. Our successional stages are defined by current vegetation structure and should be strongly correlated with stand age and with length of time since the last stand-replacing disturbance, but we could not verify this assumption. Furthermore, the successional stages are less useful for describing uneven-aged stands that are common in southwest Oregon and on the eastside, and do not reflect the effects of selective timber harvesting or other factors that influence tree density and characteristics. Chronosequence studies, in which space is substituted for time, also have inherent limitations for assessing disturbance effects. The best data for describing dead wood dynamics will come from repeated measurements of the permanently established inventory plots. Rates of snag decomposition and fall from remeasurement of FIA plots in western Washington already have been used in parameterizing a dead wood dynamics model (Mellen and Ager 2002).

Our analysis also could be improved by better information on the occurrence of contrasting forest conditions within the CVS plots. While we could identify plots that straddled major land classes (forest and nonforest) and potential vegetation types (forest series), there currently is no easy way to identify different conditions such as successional stages within the series. Although algorithms could be applied to the basic tree data, no such computer programs have been developed and their efficacy is unknown. Furthermore, there is no way to identify multiple conditions within sample points on the CVS plots. As a result of not identifying multiple structural conditions, some of our plot-level estimates of dead wood and classifications of habitats and structural conditions represent averages across contrasting conditions. This introduces an unknown level of error into our regional-level weighted means, but we do not think this error is sufficient to compromise our overall findings.

Management Implications

Regional summaries of current amounts of dead wood have several potential applications to forest management, planning, and policy. One important use is in broad-scale assessments of wildlife habitat. In developing management guidelines for Federal lands, or in evaluating forest practice regulations or incentive programs for state and private lands, managers and planners can compare current amounts of dead wood to those needed by wildlife species, and to the basic capabilities of the land to produce dead wood over time. Such management guidelines currently are based on very limited scientific data. Comparisons of our estimates to those reported in most wildlife studies are complicated by the fact that our estimates represent average conditions within a habitat at the regional level rather than around specific nest sites (see earlier discussion) (Marcot and others 2002). Furthermore, although we present data on dead wood abundance, management actions may best be focused on the ecological processes that lead to development of these forest structures rather than on the structures themselves. In this regard, a major challenge for managers is that current disturbance regimes and current patterns of dead wood following decades of fire suppression may be vastly different from presettlement conditions. And lastly, management decisions will require decisions on how to spatially distribute dead wood across stands and landscapes, and guidance on such issues cannot be derived from sample-based inventories.

Information on regional patterns of dead wood currently is being incorporated into the DecAID model (Mellen and others 2002), which will help guide managers in considering dead wood and processes of decomposition in forest management. The regional inventory database contains information on occurrence of pathogens such as stem decays and root diseases that contribute dead wood. In addition, the data contain important information about the range of variability in dead wood—both historically and in the current landscape. The range of variability in dead wood abundance that is present among plots in the region can help guide distribution of dead wood within a large landscape or watershed being managed. However, caution must be exercised in using the regional plot data, which sample current conditions, to describe the historic range of conditions in dead wood. Important data on site history is lacking, as discussed earlier. Even if plots in "natural" forest could be identified, current levels of dead wood have been altered to an unknown degree by fire suppression and other human influences. On the eastside in particular, current levels of dead wood may be elevated above historical conditions due to fire suppression and increased mortality, and may be depleted below historical levels in local areas burned by intense fire or subjected to repeated salvage and firewood cutting. Plot data from natural forests on the westside, where fire return intervals are longer (Agee 1993) may provide a reasonable approximation of historical conditions.

At the forest policy level, broad-scale assessments of down wood are needed to address Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests, developed through the Montreal Process. Although dead wood was not considered in the first national-level assessment, dead wood abundance will be addressed in the first assessment of forest sustainability to be conducted by any state in the U.S. by the Oregon Department of Forestry (Birch 1999).

Acknowledgments

Regional ecological analyses such as this one depend on a group of professionals in the regional forest inventory programs, who are too numerous to list. We also rely on the ongoing programmatic commitment by the USDA Forest Service and USDI Bureau of Land Management for including ecological data in regional forest inventory and monitoring programs. We thank David Azuma, Lisa Bate, Andy Gray, Mark Harmon, Bruce Hostetler, Jerry Korol, Kim Mellen, Martin Raphael, and Tom Spies for their helpful comments on earlier versions of this paper.

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Appendix A—*Scientific and common names of tree species mentioned in this paper.*

Scientific name	Common name
Abies amabilis (Dougl.) Forbes	Pacific silver fir
Abies concolor (Gord. & Glend.) Lindl.	White fir
Abies grandis (Dougl.) Forbes	Grand fir
Abies lasiocarpa (Hook.) Nutt.	Subalpine fir
Abies magnifica var. *shastensis* Lemmon	Shasta red fir
Abies procera Rehder	Noble fir
Chamaecyparis lawsoniana A. Murray	Port-Orford cedar
Chamaecyparis nootkatensis (D. Don) Spach	Alaska yellow-cedar
Juniperus occidentalis Hook.	Western juniper
Larix lyallii Parl.	Subalpine larch
Lithocarpus densiflorus (Hook. & Arn.) Rehder	Tanoak
Picea engelmannii Parry	Engelmann spruce
Picea sitchensis (Bong.) Carr.	Sitka spruce
Pinus albicaulis Engelm.	Whitebark pine
Pinus contorta Dougl.	Lodgepole pine
Pinus ponderosa Dougl.	Ponderosa pine
Pinus jeffreyi Grev. & Balf.	Jeffrey pine
Populus tremuloides Michx.	Quaking aspen
Pseudotsuga menziesii (Mirbel) Franco.	Douglas-fir
Quercus chrysolepis Liebm.	Canyon live oak
Quercus garryana Dougl.	Oregon white oak
Quercus kelloggii Newberry	Black oak
Thuja plicata Donn.	Western redcedar
Tsuga heterophylla (Raf.) Sarg.	Western hemlock
Tsuga mertensiana (Bong.) Carr.	Mountain hemlock

The DecAID Advisory Model: Wildlife Component[1]

Bruce G. Marcot,[2] Kim Mellen,[3] Susan A. Livingston,[4] and Cay Ogden[5]

Abstract

The wildlife component of DecAID is based on a thorough review, analysis, and synthesis of the empirical literature on wildlife-dead wood relations. We developed the wildlife component by compiling data on snag and log size, snag density, and amounts of down wood related to individual species or groups of wildlife species as presented in the literature, for various habitats and types of wildlife use (breeding, feeding, roosting). The wildlife use data are arranged in three cumulative species richness curves representing means and plus or minus one standard error (or equivalent variant). The curves can be consulted to determine which species or groups are provided for snag or down wood at three statistical levels, and the amounts and sizes of snags and down wood needed to achieve a specified wildlife objective of providing for specified species, or some percent of species, at a specified statistical level. Other components of the DecAID model can then be consulted to determine hazards or mitigation for risks of fire and contribution of insects and disease to the dead wood component, and to provide for fungi and non-pest invertebrates associated with snags and down wood.

Introduction

The DecAID model is a decision-aiding advisory system being developed under the aegis of the USDA Forest Service's Pacific Northwest Region (Portland, Oregon), and the multiagency Washington-Oregon Species-Habitat Project (SHP). "DecAID" (as in "decayed" or "decay aid") will provide managers with a synthesis of all available empirical data on the relations between wildlife and wood decay elements, principally snags and down wood, in the U.S. Pacific Northwest. The model is intended to update existing regional databases and advisory models, including those of Thomas and others (1979), Marcot (1992), and others.

The DecAID model will help managers determine which wildlife species might be provided for by specific snag and down wood amounts and sizes, the amounts and

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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sizes needed to meet specified species management objectives, and the amounts and sizes expected under natural and managed conditions based on inventory data. The model also will provide information about fungi associated with dead wood and insects and diseases as disturbance agents affecting recruitment of dead wood.

This paper is one of a series of four papers in this proceedings pertaining to the DecAID model (see Mellen and Marcot [2002] for an overview of the entire DecAID model structure and components). This paper discusses the wildlife component.

Methods[6]

DecAID was designed to include empirical and all currently available data; address down wood as well as snag relations; and provide a more statistical, risk-analysis basis for assessing and managing snags and down wood for wildlife.

Step 1: Literature Review

We first conducted a thorough review of literature on empirical studies of wildlife associations with snags, partially dead trees, and down wood. We focused on studies conducted within Washington and Oregon, as well as studies in adjacent states and Canadian provinces if local studies of species or habitats were not available. We included publications in journals, books, conference proceedings, theses and dissertations, and agency publications and white papers that had undergone at least some peer review. We also obtained unpublished data from scientists currently working with dead wood issues.

Step 2: Data Synthesis

We compiled all available data on species use of snags and down wood from these papers. This involved summarizing nearly 200 papers. The data from these papers were synthesized into a master spreadsheet, listing the following information:

- For snags: snag density, decay class, dbh (diameter at breast height), height, snag species.
- For down wood: amount of down wood (volume/ha, no. logs/ha, percent cover, etc.), decay class, diameter, length, and tree species.
- For both snags and down wood: user species (e.g., wildlife or fungi), type of use (breeding, feeding, resting, denning), stand age and structure, wildlife habitat type, geographic location, explanatory comments, and source citation.

Next, we abstracted data from each study by SHP wildlife habitat type and habitat structure and by individual species or species group depending on how they were reported. Habitat types constitute an array of 31 wildlife habitats (24 terrestrial and 7 coastal and marine) developed by the SHP (Trevithick and O'Neil 1999). We were able to find data for seven of the forested wildlife habitat types. Habitat structures pertain to successional and structural stages of the wildlife habitat types

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[6] The data and statistics presented in this paper have been updated since this paper was presented. Specifically, methods now entail use of tolerance intervals, instead of confidence intervals, and an expanded set of research data on species. Thus, tables and figures in this paper should be viewed as examples of methods and not final analyses.

and were also developed by the SHP. We combined habitat structures into two categories, post-disturbance (i.e., post-fire or post-harvest) and forested, because most studies did not report habitats and structures in any finer resolution.[7]

Examples presented here pertain to two SHP forest habitat types in Washington and Oregon: (1) Eastside Mixed Conifer Forest, which comprises productive closed upland forests east of the Cascades, including forests of montane Douglas-fir *(Pseudotsuga menzeisii),* grand fir *(Abies grandis),* western redcedar *(Tuja plicata),* and western hemlock *(Tsuga heterophylla)* in the east Cascade Mountains, Okanogan Highlands, and Blue Mountains; and (2) Westside Lowlands Conifer/Hardwood Forest, which comprises lowland to low montane upland forests of western hemlock, western redcedar, Douglas-fir, Sitka spruce *(Picea sitchensis),* red alder *(Alnus rubra),* Port-Orford cedar *(Chamaecyparis lawsoniana),* and bigleaf maple *(Acer macrophyllum)* in western Washington, the Coast Range of Oregon, the western slopes of the Cascade Mountains in Oregon, and around the margins of the Willamette Valley in Oregon (Trevithick and O'Neil 1999). The examples presented here focus on post-fire structures in Eastside Mixed Conifer Forest, and forested structures in Westside Lowlands Conifer/Hardwood Forest, for nesting/breeding *(appendix A).*

For each combination of SHP wildlife habitat type and habitat structure, we recorded an array of data pertinent to each individual species or species group reported in each study (see below and *tables 1-4*), although data were not available for all wildlife habitat types or habitat structures. In this way, we could track the interpretation of each data point back to its source and understand the basis of its value. This would later prove essential in interpreting the resulting patterns across species.

The main data recorded from each study was the mean, mean minus 1 standard error (SE), and mean plus 1 SE, of snag density, snag dbh, down wood percent cover, or down wood diameter, for each individual species or species group, in each combination of habitat type and habitat structure. We also recorded the sampling basis for these data, the location of each study, and the statistical significance of use-availability analyses or regressions if the data were so derived and reported. We noted when studies provided multiple values from different study sites within the same habitat types and structures.

Step 3: Development of Cumulative Species Tables and Graphs into Cumulative Species Curves

We interpreted three statistical levels of data from our synthesis of the literature. We referred to mean minus 1 SE, mean, and mean plus 1 SE as low, moderate, and high statistical levels, respectively. These three levels refer to the degree to which statistical values of snag or down wood amount and size include values reported in the literature. Statistically, means minus 1 SE represent 32 percent of the reported values, means represent average values, and means plus 1 SE represent 68 percent of the reported values.

All values for each combination of wildlife species, wildlife habitat type and habitat structure, and data level (low, moderate, and high, respectively) were

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[7] This was later changed to three habitat structures—small/medium trees, open canopy, and large trees—as more data became available.

averaged (further versions will include weighted averages based on sample sizes). We put this summary of data from each study into spreadsheet tables and sorted wildlife species in order of increasing values of snag density, snag dbh, down wood percent cover, and down wood diameter, for each of the three data levels. In this way, for each wildlife habitat type and structure, we graphed curves of cumulative species richness as functions of snag density, snag dbh, down wood percent cover, and down wood diameter.

The cumulative species curves summarize the findings among species from different studies often conducted in different locations, time periods, and conditions. The curves are strictly not functions or regressions. Thus, the curves should not necessarily be interpreted as representing an increase in species richness on a given site or stand, given increases in size or density of wood decay elements. Rather, the curves should be used to suggest overall potential, individual species' use of wood decay elements across broader geographical scales, such as within watersheds or larger areas.

Step 4: Interpretation of the Cumulative Species Curves into Potential Management Guidelines

The final step entailed interpreting the cumulative species curves in terms of potential management guidelines to meet objectives for snag and down wood management for wildlife. This entailed comparing the cumulative species curves and species data with data on inventory conditions of snags and down wood from unharvested stands in each wildlife habitat type and structure (Ohmann and Waddell 2002). From this comparison, we derived a reasonable set of potential management guidelines for balancing snag density and dbh and for down wood percent cover and diameter. Because local site conditions and management histories vary greatly and other people may interpret the cumulative species curves differently, we also encourage managers to do their own inspection of the data and curves to validate our interpretation or to provide their own.

Results and Examples

Some examples will help explain the process and the form of the results. The full set of cumulative species curves for all species and habitats will be presented elsewhere.

Snag Density

Example data on wildlife use, for nesting and breeding, by snag density are presented in *table 1.* Because published studies are not available on wildlife use by snag density for nesting or breeding in post-fire structures of Eastside Mixed Conifer Forest in Washington and Oregon, we deferred to a similar study in mixed-conifer forests of south-central Idaho. Data on 8 bird species were available from one study there, depicting snag densities observed at nest sites in post-fire habitat structures (Saab and Dudley 1998). For some species, multiple values of snag densities are available in different study or treatment areas; these are shown in *table 1* and are averaged for later use in the cumulative species curves.

For example, snag density data were presented by Saab and Dudley (1998) on hairy woodpecker (see *appendix A* for scientific names) from three treatment areas. Mean values of snag density minus 1 SE ("low" statistical level) in these three areas were 48, 77, and 102 snags/ha; mean values ("moderate" statistical level) were 68, 89, and 118 snags/ha; and mean values plus 1 SE ("high" statistical level) were 84, 101, and 135 snags/ha. For each statistical level, we averaged the values across the 3 treatments—that is, 76, 92, and 107 snags/ha corresponding to low, moderate, and high statistical values, respectively—to use in the cumulative species curves.

This first example is one of the simplest cases, as all data came from one study and all values represented statistically significant selection by each species for snag densities. Further, all values represented snag densities at *nest sites* instead of *stand-wide averages*, which we interpret to mean snag densities within what may have been local snag clumps that were selected by the species reported. This last point is an important distinction because it has great bearing on interpreting the literature for devising management guidelines for snag (and down wood) densities, that is, whether reported densities should be applied stand-wide or in locally dense clumps. We further address this below.

Table 1 also presents a more complex case of combining data on wildlife use, for nesting and breeding, of snag density for nesting or breeding in Westside Lowland Conifer/Hardwood Forest. In this case, the literature did not cleanly separate various forest habitat structures (successional or structural stages) but rather reported from studies conducted in various structures in mixed forest age classes. Eight studies were available, covering seven species and two species groups. Some studies, such as McComb (1991), did not report means and SEs of snag density values, but rather we interpreted values based on their regression analyses. Studies reporting variation reported either SE or standard deviation (SD); we recorded and used what was reported. Some studies reported snag density at nest sites, others were based on stand averages, and still others reported regressions across study areas (in one case based on only hard snags). We used the closest available information to populate the data tables. Dealing with data reported in disparate ways is a perennial problem in statistics when combining information across studies (e.g., Draper and others 1992). Our approach was to record the data that were presented and to footnote the specific conditions from each study (e.g., *table 2*).

The example data from *table 1* on wildlife use of snag density for our two example habitat types were then sorted by increasing value for each of the statistical levels, and plotted on curves *(figs. 1, 2).* These example cumulative species curves show the number of wildlife species or species groups as a function of, in this case, snag density.

The cumulative species curves should be interpreted with due caution because the underlying data were reported in several different ways. For example, in Eastside Mixed Conifer Forest, post-fire structures *(fig. 1),* two sets of cumulative species curves represent snag densities for different snag size classes as reported in the literature: snags > 23 cm dbh and snags > 53 cm dbh. It is important to separate snag size classes, where possible, because, in general, smaller snags tend to be more numerous than larger snags, and snag density use and selection by the same wildlife species can vary by snag size class.

Table 1—*Example data on wildlife use by snag density in two example habitats (see text for caveats and explanations).*

	No. snags/ha										
Species[1]	**Low[2]**	**Moderate[2]**	**High[2]**	**Form of data for Moderate**	**Form of data for Low, High**	**Min. dbh (cm)[3]**	**Type data[4]**	**Location**	**P value[5]**	**Plot size (ha)[6]**	**Source[7]**
Habitat type: Eastside Mixed Conifer/Ponderosa Pine Forest; Habitat structure: Post-fire; Type of use: Nesting/breeding											
BBWO	108	155	202	mean	SE	23	nest site	s-c Idaho	0.001	0.04	Saab and Dudley 1998
HAWO	48,77,102	68,89,118	84,101,135	mean	SE	23	nest site	s-c Idaho	0.001	0.04	Saab and Dudley 1998
LEWO	54,58	60, 64	66,70	mean	SE	23	nest site	s-c Idaho	0.001	0.04	Saab and Dudley 1998
LEWO	12,15	14,18	15,21	mean	SE	53	nest site	s-c Idaho	0.05	0.04	Saab and Dudley 1998
MOBL	56,58,64	70,71,76	86,82,89	mean	SE	23	nest site	s-c Idaho	0.001	0.04	Saab and Dudley 1998
MOBL	23	31	39	mean	SE	53	nest site	s-c Idaho	0.05	0.04	Saab and Dudley 1998
NOFL	36	44	52	mean	SE	53	nest site	s-c Idaho	0.05	0.04	Saab and Dudley 1998
NOFL	50,62,62	62,73,82	84,76,100	mean	SE	23	nest site	s-c Idaho	0.001	0.04	Saab and Dudley 1998
WEBL	53,61,98	71,68,125	152,81,84	mean	SE	23	nest site	s-c Idaho	0.001	0.04	Saab and Dudley 1998
WHWO	50	62	75	mean	SE	23	nest site	s-c Idaho	0.001	0.04	Saab and Dudley 1998

(*table 1* continued)

Habitat type: Westside Lowland Conifer/Hardwood Forest; Habitat structure: Various (mixed forest age classes); Type of use: Nesting/breeding

Species[1]	No. snags/ha Low[2]	Moderate[2]	High[2]	Form of data for Moderate	Form of data for Low, High	Min. dbh (cm)[3]	Type data[4]	Location	P value[5]	Plot size (ha)[6]	Source[7]
BTWO	26.29	32.45	38.61	mean	SE	25	stand avg	w OR Cascades	0.065	0.08	C. Maguire, pers. comm.
CNB	0.5	not avail.	97	n/a	range	13	regression	Olympic Peninsula	0.01	n/a	Zarnowitz and Manual 1985
CNB	18	19	20	mean	SE	50	nest site	OR Coast Range	0.001	0.2	Nelson 1988
CNB	22	24	26	mean	SE	20-49	nest site	OR Coast Range	0.001	0.2	Nelson 1988
DEMO mammals	not avail.	25.61	not avail.	mean	not given	25	stand avg	w OR Cascades	n/a	0.08	C. Maguire, pers. comm.
DOSQ	21.62	25.53	29.44	mean	SE	25	stand avg	w OR Cascades	0.8314	0.08	C. Maguire, pers. comm.
GMGS	18.21	24.03	29.85	mean	SE	25	stand avg	w OR Cascades	0.8954	0.08	C. Maguire, pers. comm.
NFSQ	9.2	not avail.	20	n/a	range	50	stand avg	OR Coast Range	0.032	n/a	Corn and Bury 1991
NFSQ	21.62	25.53	29.44	mean	SE	25	stand avg	w OR Cascades	0.8314	0.08	C. Maguire, pers. comm.
PIWO	3	16	29	mean	SD	40	nest site	OR Coast Range	n/a	0.3	Mellen 1987
PIWO	4	21	38	mean	SD	15-40	nest site	OR Coast Range	n/a	0.3	Mellen 1987
TOCH	1	not avail.	8	n/a	range	50	regression--hard snags	OR Cascades	0.002	n/a	Rosenburg and Anthony 1993
TOCH	not avail.	17	not avail.	mean	not given	50	stand avg	OR Coast Range	n/a	0.035	Carey and others 1996

[1] See *table 2* for all footnotes contained in *tables 1 and 2*.

Table 2—*Example data on wildlife use by snag size (diameter at breast height, dbh) in two example habitats.*

	Snag dbh (cm)[7]		
Species[1]	**Low[2]**	**Moderate[2]**	**High[2]**
Habitat type: Eastside Mixed Conifer/Ponderosa Pine Forest **Habitat structure: Post-fire** **Type of use: Nesting/breeding**			
AMKE	46,54	50,59	54,63
BBWO	20,22,30.35	23,28,32,40	26,35,35,45
BRCR	72	not avail.	89
CNB	20,34	35,39	36,58
EUST	30	31	32
HAWO	24,32,34,35	28,34,35,53	32,36,37,70
HOWR	28	30,30	31,32
LEWO	40,43	45,48	46,56,78
MOBL	22,29,32	31,32,34,32	36,36,40
NOFL	30,40,41,34	34,41,43,37	39,42,45,52,40
NTWO	21,30	22,31	32
RBNU	32	34	36,56
TRSW	31	32	33
WEBL	33	35	36
WHWO	33	37	42
Habitat type: Westside Lowland Conifer/Hardwood Forest **Habitat structure: Various (mixed forest age classes)** **Type of use: Nesting/breeding**			
AMMA	not avail.	81,[80][9]	not avail.
BRCR	41,75	84	92
CBCH	32,58,103	76,94,103,108	113,120,130
CNB	49,76	[50][9],83	117
HAWO	33,41,49,62	[50][9],58,72,74,80	82,83,92,107,112
NFSQ	86,65,60,39,71	[50][9],64,77,93,42,74	100,89,67,44,77
NOFL	41,46,[86][8]	53,61,78,96	65,106,109,128
PCE	[83][8]	[50][9],88	92
PIWO	44,59	67,69,78,88	75,94,100

(*table 2* continued)

Habitat type: Westside Lowland Conifer/Hardwood Forest
Habitat structure: Various (mixed forest age classes)
Type of use: Nesting/breeding

PIWO	72	78	84
PYWO	32,54	56	79
RBNU	40,75	[50] [9],71,82	89,102,118
RBSA	52,[103] [8],76	80,101,[113] [10]	109,123
SCNB	63,94	98	103
WIWR	not avail.	93	not avail.

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[1] See *appendix A* for species names and codes.

[2] Low = mean - 1 SE; Moderate = mean; High = mean + 1 SE. Multiple entries denote different study sites.

[3] Min dbh refers to the lower value of snag dbh reported in the study. This is an important factor to track because, generally, larger snags are less numerous than smaller snags.

[4] Type data refers to whether the snag densities were reported only at nest sites ("nest site"), throughout the stand ("stand avg"), or for all study sites combined ("regression").

[5] P value refers to the reported statistical outcome of use-availability analyses. P values > 0.05 pertain to studies that failed to demonstrate selection for particular snag densities; however, snag data from these studies are still useful for describing stands in which the species was observed to be present, and thus are included here.

[6] Plot size refers to the area of the sample plots in which snag density was calculated.

[7] Various sources.

[8] Value is mean - 1 SD, even though it is higher than some mean values.

[9] Preference data; redundant with utilization data, so not included in further analyses.

[10] Value is mean from 1 study, even though it is higher than some means + SD.

[11] Value is anomalously high and based on snags > 13 cm dbh, and thus not included in the cumulative species curve.

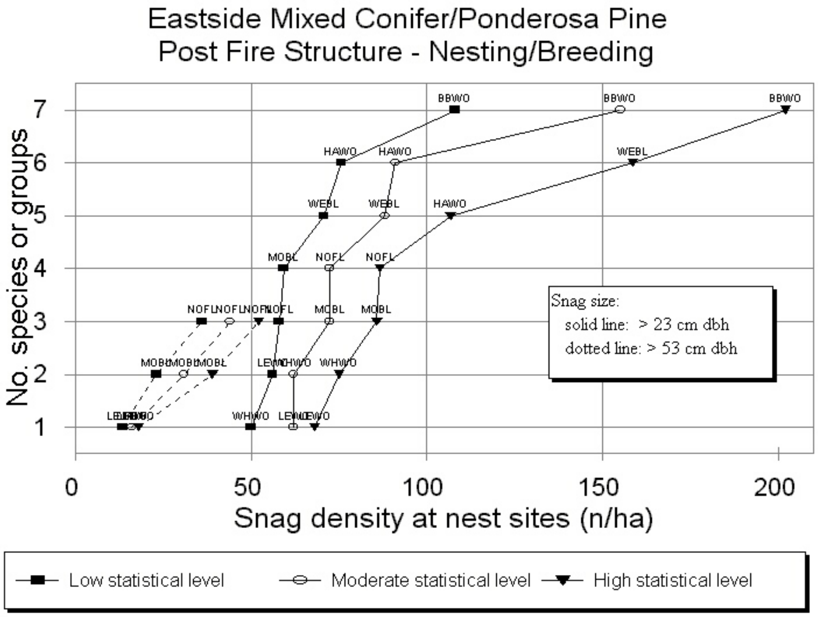

Figure 1—Example cumulative species curves of snag density in Eastside Mixed Conifer/Ponderosa Pine Forest, post-fire structural condition, for nesting/breeding use by wildlife, in eastern Washington and Oregon.

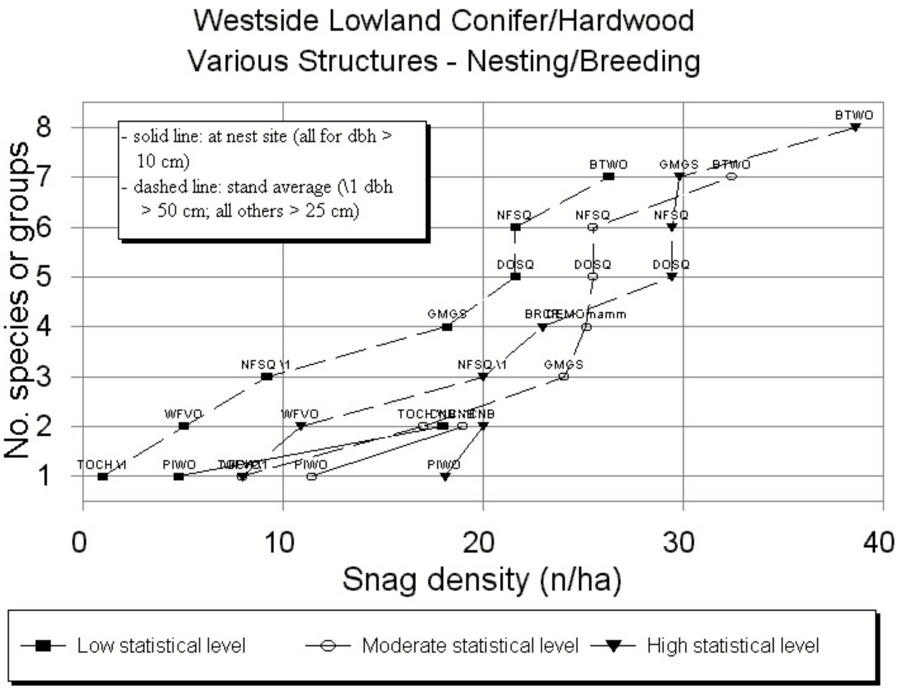

Figure 2—Example cumulative species curves of snag density in Westside Lowland Conifer/Hardwood Forest, various structural conditions, for nesting/breeding use by wildlife, in western Washington and Oregon.

Because all example data for Eastside Mixed Conifer Forest came from nest sites, so these particular cumulative species curves *(fig. 1)* could all be interpreted as representing snag densities within local snag clumps at nest sites, not necessarily as stand-wide averages. In contrast, in Westside Lowland Conifer/Hardwood Forest *(fig. 2),* the literature presented data not by snag size class, but different studies reported snag densities at nest sites (this may be in local snag clumps) or as stand-wide averages, and we show these in different sets of curves. The values of snag density are generally higher in snag clumps than for stand-wide averages *(fig. 2);* this makes intuitive sense. Another data artifact appears in *figure 2,* where the curves for moderate and high statistical levels for stand averages cross. This occurs because the data were not reported in the literature the same way for the same species at each statistical level; thus, attention needs to be given to the individual species on the data points in each curve.

The cumulative species curves can be read in two ways for management use: 1) by beginning with a known or expected snag density and reading up from the x-axis to the curves to determine which species, and what fraction of all reported species, would be provided at different levels of confidence by managing within observed values; or 2) by beginning with a specific species management target, such as for specific species or a specific fraction of all reported species, finding those target species on each cumulative species curve or along the y-axis, and reading down to the x-axis to determine what snag density would correspond to that reported in the literature at a particular statistical level (low, moderate, or high).

For example, presume that one is managing some Eastside Mixed Conifer forest stand for some purpose such as fuels reduction, and that it is expected that such silvicultural treatments will result in providing for snags > 23 cm dbh in local clumps averaging 100 snags/ha within each clump. Consulting *figure 1,* for a density of 100 snags/ha, at > 23 cm dbh, one would determine that this snag density would provide for four of the seven reported nesting or breeding species at the high statistical data level, and six of the seven nesting or breeding species at both the moderate and low levels. Further, one can determine which conditions for each species would, and which would not, match conditions reported in the literature. For example, at the high statistical level, the proposed management conditions in this scenario would fit the reported use patterns for all species except hairy woodpecker, western bluebird, and black-backed woodpecker; studies suggest that these three species use and select for higher snag densities in recent burns, although they might select for different conditions elsewhere (Bunnell, pers. comm.).

Alternatively, one could begin with a specific management goal, such as providing for all reported snag-using species at a particular statistical level. For example, in Eastside Mixed Conifer Forest *(fig. 1)* this would entail providing local clumps of snags > 23 cm dbh with densities within the clumps of at least 110 snags/ha at low statistical levels of observed species' nesting or breeding usage, 155 snags/ha at moderate levels, and 200 snags/ha at high levels. (The question of what constitutes a clump, how many clumps to provide, and how to distribute a clump is addressed below.) In Westside Lowland Conifer/Hardwood Forest *(fig. 2),* meeting the nesting or breeding use patterns of all reported species or species groups would entail providing within-clump average snag densities (the dashed lines in *fig. 2)* of about 26 to over 38 snags/ha. Also, the cumulative species curves for the two forest habitats explored here suggest that secondary cavity-using species such as northern flying squirrel and western bluebird may select for higher snag densities than many of the primary cavity-excavating species. (Values presented here and below are only examples of use of DecAID; the final model likely will have different values.)

Snag Diameter

Data on wildlife use, for nesting or breeding, by snag diameter (dbh) are far more numerous than are data on snag density. Data on 15 individual species or species groups are available for Eastside Mixed Conifer Forest and 14 species or groups for Westside Lowland Conifer/Hardwood Forest *(table 2).* However, again, the literature inconsistently reports these data. Most studies reported actual dbh of snags used by a species for a specific function (e.g., nesting, roosting, foraging). Preference studies reported snag dbh in various ways: by disparate snag dbh size classes or categories; by snags at nest sites, as averaged throughout the stands, or as regressions across study areas; by different sampling designs; and by snags generally occurring within the stand or as selected by the species (selection data).

These differences in reporting make overall interpretation of patterns of snag diameter use by nesting or breeding species difficult. However, one can use cumulative species curves *(figs. 3, 4)* for these two example habitats in the same way as with the snag density curves—that is, to determine what fits reported patterns. Comparing the curves for two habitats shows that in general, species use much larger snags in the Westside forest type than in the Eastside forest type for nesting or breeding; this makes intuitive sense, as Westside forests typically currently have larger diameter mature trees and snags, given higher rainfall and more productive tree-growing environments there. The example curves suggest that, to meet the use patterns of all reported individual species and species groups, snags of at least 72 to 89 cm dbh are needed in Eastside Mixed Conifer Forest, post-fire structures *(fig. 3)* and 92 to 121 cm dbh in Westside Lowlands Conifer/Hardwood Forest, various forest structures *(fig. 4),* for low to high statistical levels, respectively.

Also, the cumulative species curves suggest that secondary cavity-using species may select larger diameter snags than many of the primary cavity-excavating species. This is especially true with Brown Creeper and American Kestrel in the Eastside forests *(fig. 3),* and with Chestnut-backed Chickadee, Red-breasted Nuthatch (which can also excavate cavities), and other secondary cavity-nesting birds (species group "SCNB") in Westside forests *(fig. 4)*. (Note that Winter Wren also appears in *fig. 4.* This species was shown to correlate with large snags in the associated study, although the species generally does not use snag cavities per se. The correlation may pertain to use of down wood at the base of the snags or sloughing bark as nesting or hiding sites. As well, Brown Creeper often uses sloughing bark higher up on the bole of large diameter, tall snags and live trees, and does not typically use cavities per se.)

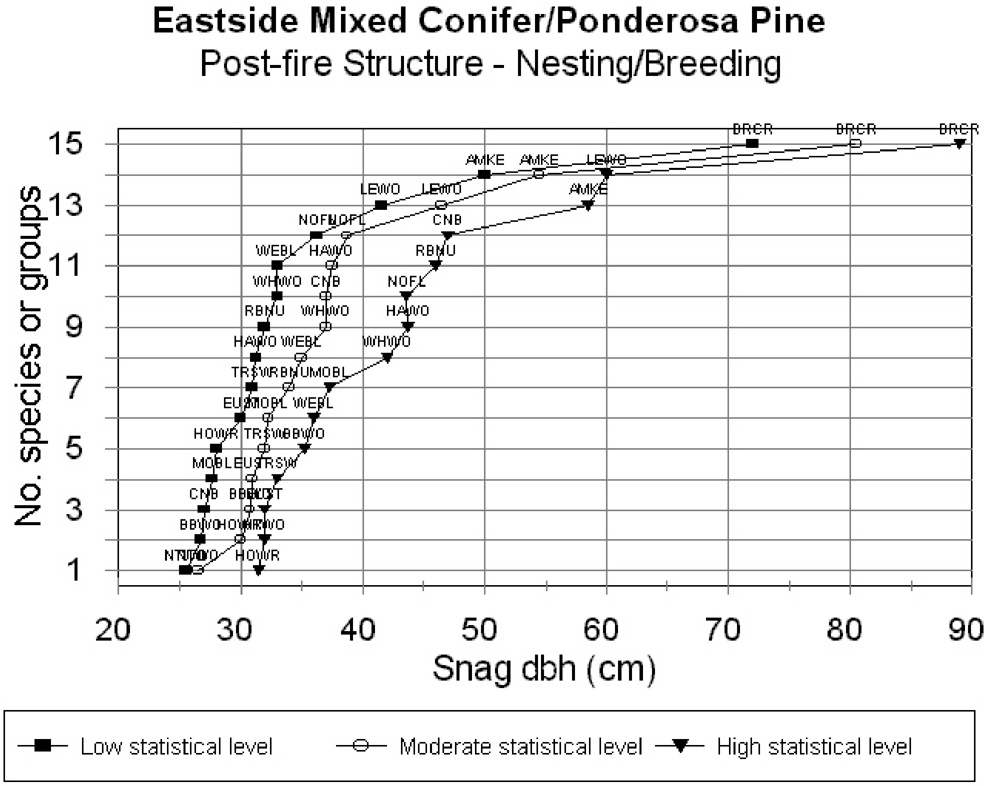

Figure 3—Example cumulative species curves of snag diameter in Eastside Mixed Conifer/Ponderosa Pine Forest, post-fire structural condition, for nesting/breeding use by wildlife, in eastern Washington and Oregon.

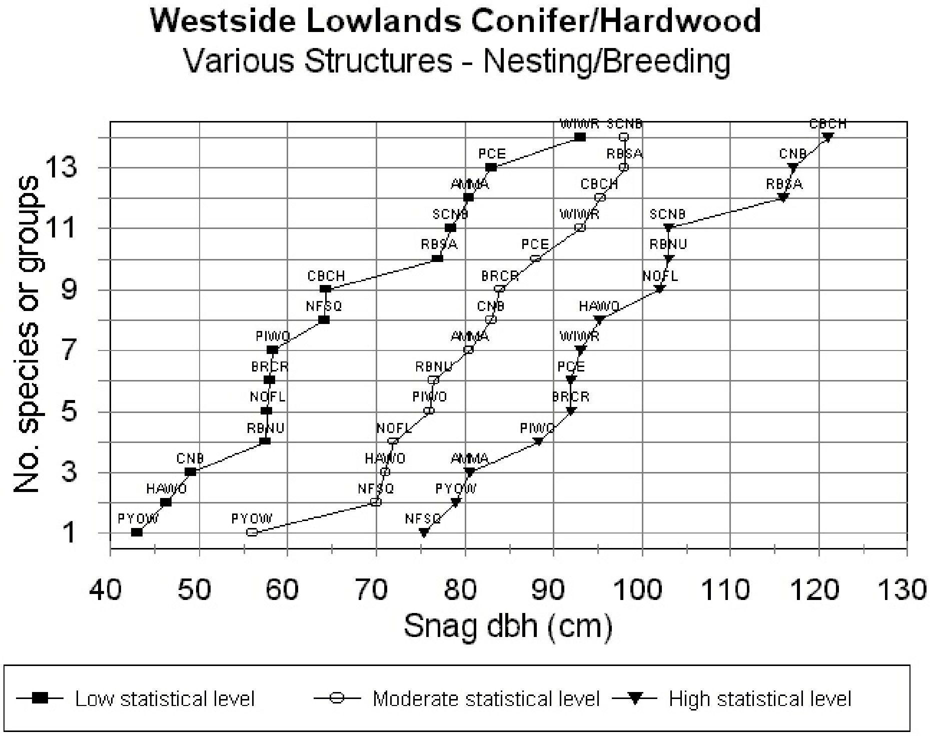

Figure 4—Example cumulative species curves of snag diameter in Westside Lowland Conifer/Hardwood Forest, various structural conditions, for nesting/breeding use by wildlife, in western Washington and Oregon.

Down Wood Percent Cover

Overall, scant data are available on wildlife use of down wood. One of the major problems is that down wood is reported in the literature in too many disparate ways: as percent ground cover, and as number of pieces, volume, density, and mass per unit area. Fuels managers prefer estimates of volume and mass, whereas for wildlife use percent ground cover may be the best single estimator (Torgersen, pers. comm.; Carey, pers. comm.). In British Columbia, down wood percent cover was a useful unit for fungi, most cryptogams, and small mammals, although down wood volume seemed more useful for Plethodon salamanders (Bunnell, pers. comm.). We used inventory data to develop regression equations to convert among these units, although such conversions introduce unknown errors in estimation.

In Eastside Mixed Conifer Forest, only two studies provided data on wildlife use of down wood cover, and one of these pertains to fungi species. The story is far better in Westside Lowland/Conifer Hardwood Forest, where 5 studies provide data on 23 species and 2 species groups *(table 3).* The example cumulative species curves *(figs. 5, 6)* suggest that, to provide for all reported species at high statistical levels, over 4 percent down wood cover in Eastside forests and 20 percent in Westside forests would be necessary to fall within observed values of species use and selection. At least for Westside forests, these values are much greater than the 0.5 to 1 percent typically specified in the Northwest Forest Plan, but, as with snag densities, they might pertain to cover within locally dense clumps of down wood, not necessarily stand-wide averages. This is a vital distinction for management.

Table 3—*Example data on wildlife use by down wood percent cover in two example habitats.*

	Percent cover down wood									
Species[1]	**Low**[2]	**Moderate**[2]	**High**[2]	**Mininum diameter (cm)**[3]	**How measured**	**P value**[4]	**Log decay class**[5]	**Plot size**[6]	**Data type**	**Source**
Habitat type: Eastside Mixed Conifer Forest; Habitat structure: Various forest structures; Type of use: Presence and density										
FUNG	0.7	1.1	1.4	7.5	not given	n/a	1-5	n/a	threshold density	Graham and others 1994
PIWO	1.6	3.2	4.7	15	not given	n/a[10]	not given[11]	0.4 ha	foraging use	Bull and Holthausen 1993
Habitat type: Westside Lowland Conifer/Hardwood Forest; Habitat structure: Various forest structures; Type of use: Presence, abundance, and nesting										
BTWO	5.54	7.35	9.16	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
CLSA	2.1	not avail.	not avail.	10	not given	n/a	1-5	line transect	presence	Butts 1997
CLSA	5.92	6.97	8.02	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
DEMO mamm	not avail.	6	not avail.	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
DOSQ	4.5	5.3	6.1	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
DUSA	8.6	10.01	11.42	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
ENSA	7.2	9.2	11.1	10	not given	0.03	1-5	line transect	presence	Butts 1997
ENSA	4.83	5.76	6.69	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
GMGS	4.27	4.3	4.33	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
MAPG	2.69	3.12	3.55	10	transect intersection	0.0109	1-5	line transect	selection	C. Maguire, pers. comm.
MASH	6.6	8.2	9.8	10	transect intersection	0.013	1-5	line transect	selection	C. Maguire, pers. comm.
NFSQ	9.6	10	10.4	10	not given	<0.05	1-5	0.035 ha	presence	Carey and others 1999
NFSQ	5.44	6.43	8.91	10	transect intersection	0.0001	1-5	line transect	selection	C. Maguire, pers. comm.

(*table 3* continued)

Species[1]	Percent cover down wood Low[2]	Moderate[2]	High[2]	Mininum diameter (cm)[3]	How measured	P value[4]	Log decay class[5]	Plot size[6]	Data type	Source
NOSA	4.64	5.36	6.08	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
PCFR	1.78	2.28	2.78	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
PGSA	6.9	9.06	11.22	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
PIWO	4.02	4.65	5.28	20	transect intersection	0.01	1-5	line transect	foraging sites	Hartwig 1999
PJMO	6.51	8.15	9.79	10	transect intersection	0.0152	1-5	line transect	selection	C. Maguire, pers. comm.
RONE	5.69	6.9	8.11	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
SHMO	5.09	6.08	7.07	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
SMMA	5	12.5	20	10	not given	not given	1-5	not given	Abundance[7]	Carey and Johnson 1995
SPFR	not avail.	4.66	not avail.	10	transect intersection	0.0402	1-5	line transect	selection	C. Maguire, pers. comm.
SPSK	6.2	7.73	9.26	10	transect intersection	0.0402	1-5	line transect	selection	C. Maguire, pers. comm.
STWE	4.99	6.61	8.23	10	transect intersection	0.0402	1-5	line transect	selection	C. Maguire, pers. comm.
TOCH	8.3	8.6	8.9	10	not given	<0.05	1-5	0.035 ha	presence	Carey and others 1999
TOVO	3.76	4.68	5.6	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
VASH	4.7	5.6	6.5	10	transect intersection	n/a	1-5	line transect	presence	C. Maguire, pers. comm.
WRSA	7.35	9.5	11.65	10	transect intersection	0.0154	1-5	line transect	selection	C. Maguire, pers. comm.

[1] See *table 4* for all footnotes contained in *tables 3 and 4*.

Table 4—*Example data on wildlife use by down wood diameter in two example habitats.*

	Down wood diameter (cm)							
Species[1]	Low[2]	Moderate[2]	High[2]	Selection?[8]	How measured	P value[4]	Data type	Source
Habitat type: Eastside Mixed Conifer/Ponderosa Pine Forest; Habitat structure: Various forest structures; Type of use: Presence, foraging, and denning								
ABBE	not avail.	43.3	not avail.	no	large end diam.	not given	foraging	Bull 1998
ABBE	66.51	86	105.49	no	large end diam.	not given	denning	Bull and others 1999
ABBE	91.77	108	124.23	no	large end diam.	not given	denning	Bull and others 1999
PIWO	not avail.	38	not avail.	yes	not given	0.03	foraging (preference)	Bull and Holthausen 1993
PJMO	not avail.	25	not avail.	yes	not given	<0.05	size class preference	Hallet and O'Connell 1997
SRBV	not avail.	25	not avail.	yes	not given	<0.05[9]	size class preference	Hallett and O'Connell 1997
Habitat type: Westside Lowland Conifer/Hardwood Forest; Habitat structure: Various forest structures; Type of use: Presence and selection								
BTWO	28.94	31.43	33.92	yes	transect intersection	0.0012	presence	C. Maguire, pers. comm.
CLSA	50.3	52.5	54.5	yes	not given	<0.01	used/unused	Corn and Bury 1991
CLSA	27.25	29.3	31.35	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
DEMO mamm	not avail.	26.08	not avail.	no	transect intersection	n/a	presence	C. Maguire, pers. comm.
DOSQ	23.07	24.47	25.87	no	transect intersection	0.1537	presence	C. Maguire, pers. comm.
DUSA	24.9	26.8	28.7	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
ENSA	not avail.	50	not avail.	yes	not given	<0.008[9]	presence	Butts 1997
ENSA	24.53	26.07	27.61	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
GMGS	19.27	20.26	21.25	yes	transect intersection	0.0027	presence	C. Maguire, pers. comm.
MASH	28.18	30.01	31.84	yes	transect intersection	0.0258	presence	C. Maguire, pers. comm.

(*table 4* continued)

MAPG	20.68	22.2	23.72	yes	transect intersection	0.0188	presence	C. Maguire, pers. comm.
NFSQ	25.49	27.16	28.83	yes	transect intersection	0.0005	presence	C. Maguire, pers. comm.
NOSA	24.47	25.99	27.51	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
PCFR	18.3	19.77	21.24	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
PGSA	29.71	32.39	35.07	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
PJMO	25.47	27.92	30.37	no	transect intersection	0.2951	presence	C. Maguire, pers. comm.
RONE	25.49	27.37	29.25	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
SHMO	22.94	26.4	28.02	no	transect intersection	0.8764	presence	C. Maguire, pers. comm.
SPFR	not avail.	38.7	not avail.	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
SPSK	26.24	28.17	30.1	no	transect intersection	0.2368	presence	C. Maguire, pers. comm.
STWE	22.11	25.38	28.65	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.
TOVO	27.1	29.32	31.54	no	transect intersection	0.185	presence	C. Maguire, pers. comm.
VASH	24.24	25.75	27.26	no	transect intersection	>0.05	presence	C. Maguire, pers. comm.
WRSA	25.38	27.7	30.02	no	transect intersection	not avail.	presence	C. Maguire, pers. comm.

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[1] See *appendix A* for species names and codes.

[2] Low = mean - 1 SE; Moderate = mean; High = mean + 1 SE.

[3] Smallest size down log included in each study.

[4] P value refers to the reported statistical outcome of use-availability analyses.

[5] Log decay class is the category of physical decay of the down wood (Maser and others 1979). 1-3 sound, 4-5 rotten.

[6] Plot size refers to the area of the sample plots in which down wood percent cover was estimated.

[7] Presence of "large populations of most small mammals" (values not given).

[8] Selection refers to statistical demonstration of preference for size class (diameter) of down wood. "No" implies that descriptive data only were presented (no statistical preference analysis was conducted).

[9] P values and preference statistics taken from regression equations: for Hallet and O'Connell (1997), these were stepwise multiple regressions where logs > 25 cm diameter were the first significant component in the regression; and for Butts (1997) where large logs (>50 cm diameter) was the only significant component in a logistic regression equation.

[10] Recommendation, no statistics given.

[11] Reported preference for "long, dead, large logs" where large means 38+ cm diameter.

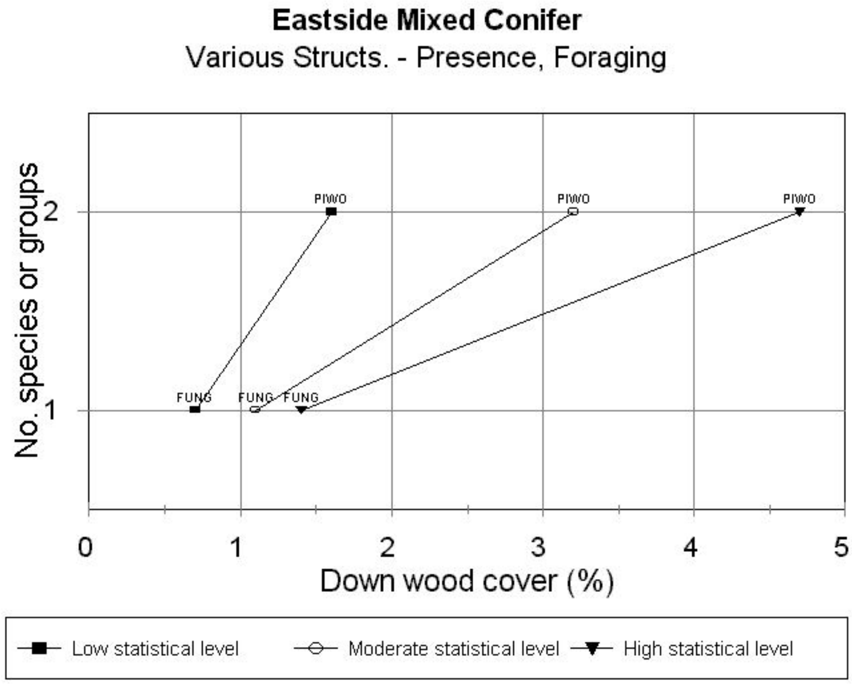

Figure 5—Example cumulative species curves of down wood percent cover in Eastside Mixed Conifer/Ponderosa Pine Forest, various structural conditions, for presence and foraging use by wildlife, in eastern Washington and Oregon. Ponderosa Pine Forest is included here and in *table 3* because the studies did not separate the two forest types.

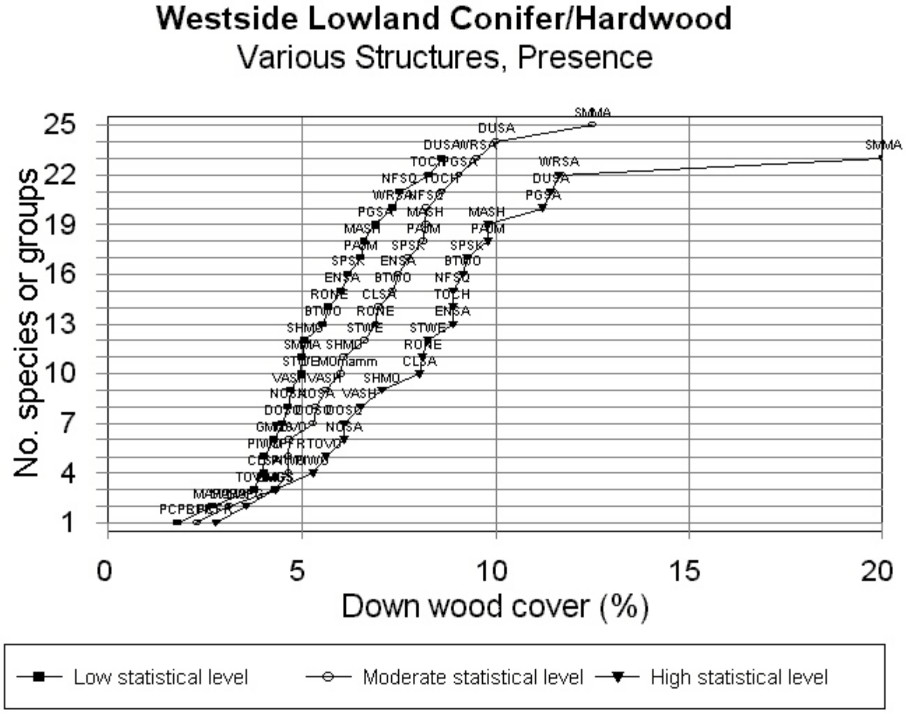

Figure 6—Example cumulative species curves of down wood percent cover in Westside Lowland Conifer/Hardwood Forest, various structural conditions, for presence and nesting/breeding use by wildlife, in western Washington and Oregon.

Down Wood Diameter

Data on wildlife use of down wood diameter also are very sparse for the Eastside Mixed Conifer Forest (3 studies, 4 species) but are somewhat better for Westside Lowland/Conifer Hardwood Forest (3 studies, 21 species and 1 species group) *(table 4)*. Diameters of Eastside down logs tend to be far larger for denning use than for foraging use *(fig. 7),* ranging up to 50 cm diameter for foraging by pileated woodpecker and over 120 cm for denning by American black bear. Diameters of Westside down logs range up to 43 cm *(fig. 8),* although data on diameter use by bears is not available there. We presume that all diameter values should be interpreted as small-end diameter, although many studies reported transect-intercept diameter or large end diameter.

Overall Interpretations

Interpreting the cumulative species data and curves for wildlife habitat management is going to be a complex process requiring knowledge of local site conditions and species' use patterns or needs. For example, interpreting the cumulative species curves independently for amounts and for sizes, of snags and down wood, may lead to incorrect estimation or conflicting projections of what is needed. Because some species select for different size classes of snags or down wood, one size does not fit all. Some combination of sizes may be needed to meet all species' use patterns.

How should one balance density and size for snag or down wood management within a stand? The overall process involves comparing and balancing snag or down wood size with snag or down wood density from the cumulative species curves, determining if this pertains to stand average values or local snag or down wood clumps, and comparing the species use data to inventory data taken in unmanaged (unharvested) stand conditions.

Here is an example with the snag data for Westside Lowland Conifer/Hardwood Forest, various forested structures. To manage for all reported nesting or breeding wildlife at high statistical levels, focusing on the species' use data representing stand averages, the stand would average about 39 snags/ha *(fig. 2)* > 25 cm dbh *(table 1, fig. 2).* This total would include at least 20 snags/ha > 50 cm dbh for northern flying squirrel *(table 1).* Also used are a few very large snags up to about 120 cm dbh for red-breasted sapsucker, chestnut-backed chickadee, and some cavity-nesting birds in general *(fig. 4)* scattered within and among the clumps, although chestnut-backed chickadee might use smaller snags that are well rotted (Bunnell, pers. comm.). Retaining any snags > 80 cm dbh would help meet needs of roosting bats and American marten as well (based on data for roosting and denning, not shown here). Amounts and sizes of snags at low or moderate statistical levels would be proportionately lower.

Values of snag or down wood density and size as interpreted from the cumulative species curves should be compared with forest inventory data (namely, the Continuous Vegetation Survey [CVS] and Forest Inventory and Analysis [FIA]) taken in unmanaged (unharvested) stand conditions (Ohmann and Waddell 2002). This provides a cross-check of the potential of the stand for producing snags and down wood in unharvested settings. For example, a preliminary analysis of inventory data in Westside Lowland Conifer/Hardwood Forest from reserved lands (representing unharvested conditions) suggests that natural densities of snags > 25 cm dbh average 48.4 and 40.0 snags/ha in young and mature stand structural classes, respectively, and snags > 50 cm dbh average 16.0 and 17.5 snags/ha in young and mature classes, respectively. These average values are close to the values derived from the cumulative species curves cited above, verifying that these may be appropriate stand-wide goals. In some cases, snags can be managed in clumps if the species' use data were summarized from studies focused on selected use of locally dense patches of snags or down wood, and if such values were significantly greater than stand averages as denoted in the inventory data.

The idealized cumulative species curves may not fit what is feasible on a given site, given its management history, current conditions, and expected future conditions. Disturbance such as stand-replacing fires, timber harvests, intermediate silvicultural treatments, and human safety management may result in snag and down wood conditions far different than expected or desired in a particular stand.

How does one balance all these issues and conditions? The answer may be in taking a broader view across stands and landscapes. It is imperative, however, to not average snag and down wood densities and sizes across too broad an area, such as across entire watersheds, potentially leaving large areas within watersheds with snags or down wood elements that are too scarce or too small to be of use by wildlife. An honest evaluation of watershed conditions, including the current condition and future capability of stands within, is a sound basis for devising reasonable management goals and expectations for snags and down wood on all lands.

Choosing Statistical Levels for Management Goals

How should one interpret the statistical levels represented by the low, medium, and high curves? It may be useful to interpret the three statistical levels as confidence levels and match them with overall goals for managing snags and down wood as one facet of habitat diversity for wildlife. Different landowners may have appropriately different expectations for diversity management, and thus for statistical levels to manage for, on various land use allocations.

For example, lands established or allocated mainly for conservation and protection of native ecosystems and wildlife communities, such as national parks and wilderness areas, could appropriately be operating at high statistical levels for amount and size of snags and down wood for wildlife. These lands are managed under the strictest set of regulations and laws for nature conservation. Usually, active forest management, especially timber harvesting, is not conducted on these particular lands, although one important exception is Managed Late-Successional Reserves under the Northwest Forest Plan.

It might be appropriate to allow a lower statistical level on other lands clearly designated for timber production and other intensive resource production uses. Such lands are subject to State Forestry Practices regulations and the Endangered Species Act, but not the Federal regulations for population viability and biodiversity management governing national forests. At the least, the information provided by the cumulative species curves in the DecAID advisory model will help determine the degree to which amounts and sizes of snags and down wood provided on various categories of land use, ownership, and allocation, match those reported in the wildlife literature and in inventory data from unharvested lands.

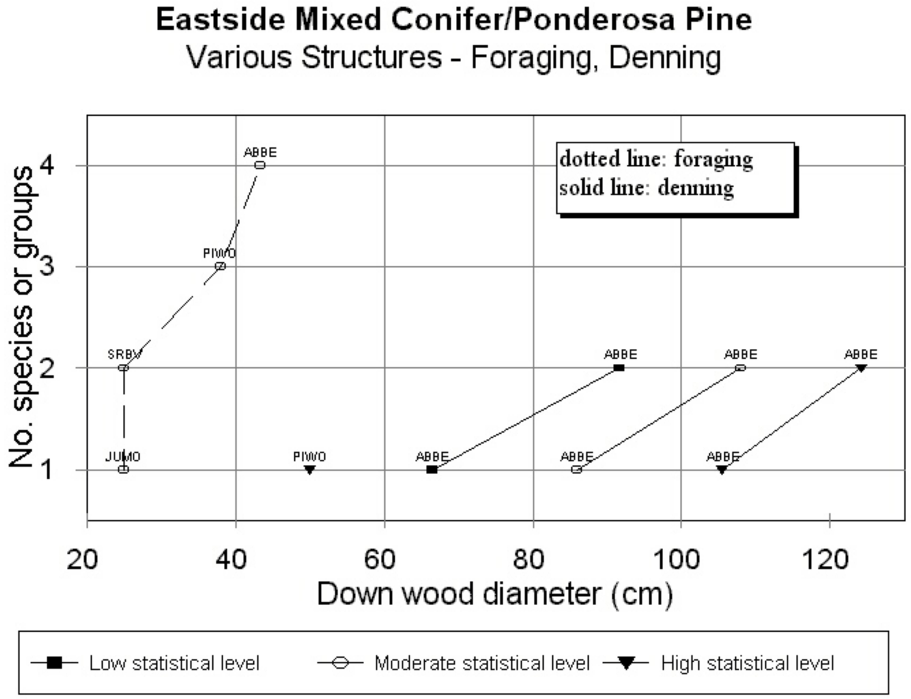

Figure 7—Example cumulative species curves of down wood diameter in Eastside Mixed Conifer/Ponderosa Pine Forest, various structural conditions, for foraging and denning use by wildlife, in eastern Washington and Oregon. Note that American black bear is represented in the denning curves twice, as data came from two different studies.

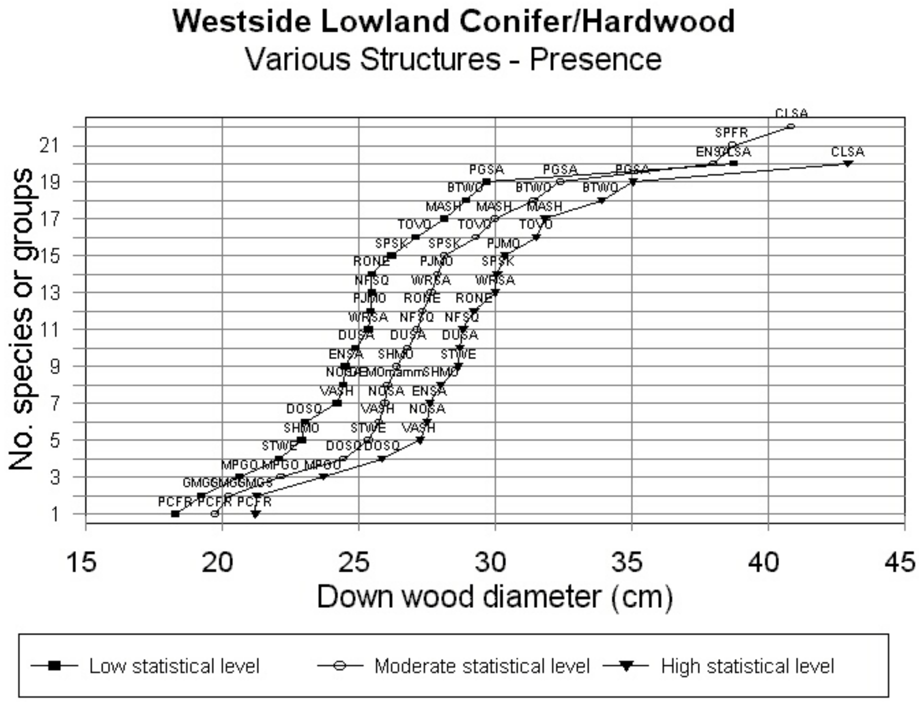

Figure 8—Example cumulative species curves of down wood diameter in Westside Lowland Conifer/Hardwood Forest, various structural conditions, for presence of wildlife, in western Washington and Oregon.

Clumping and Distribution Issues

We discussed above how we interpreted some reported snag or down wood densities as possibly occurring in local clumps instead of stand-wide averages. This interpretation seems appropriate for studies reporting densities specifically at wildlife use sites, such as nests, dens, and roosts, and especially for studies that also demonstrate selection for higher densities over stand averages.

The management question then becomes one of providing the clumps—how big, how many, and how spaced? Essentially no study has provided answers to these questions. Thus, we analyzed data on snags and down wood collected systematically in one study (Bate, pers. comm.) to determine patterns of clumping within stands. Results suggest that snags and down wood do occur in clumps, or at least nonuniformly within stands (Marcot and others 2002). In this study, observed patterns of snag and down wood distributions (number of snags or down wood pieces per line transect segment) best fit an "independent density" model. This model has fixed intervals along a line with uniform, randomly varying numbers of snags and down wood pieces, rather than a "clump-and-space" model in which uniformly randomly varying clump densities are interspersed with empty spaces that also vary randomly in size.

The better fit of empirical data on snag and down wood dispersion to the "independent density" model suggests that managers can take opportunistic advantage of site-specific occurrences of snags and down wood without having to match a particular spatial distribution pattern of clumps. This offers great flexibility to managers to provide varying local densities of snags and down wood across the ground, within and among stands. Managers would need to add the temporal dimension to this, to ensure that sufficient snag and down wood densities and sizes are provided over successional time.

In some cases, snag or down wood clumps occur because of contagious distributions of fungal rot such as *Armellaria* in conifers and *Phellinus* in aspen, or other wood decay agents. The manager may need to consider the tradeoffs and likelihoods of retaining fungal wood decay agents on further infection of sound wood.

Caveats and Cautions in Using the Cumulative Species Curves

Interpreting the Cumulative Species Curves

The cumulative species curves should not be applied to specific sites or individual stands. The curves represent only a summary of field studies and, in general, what might be expected on average across broad areas such as watersheds or larger areas. Most important, wildlife species richness might not increase as orderly as the curves suggest, on any given site, with increasing size or densities of snags or down wood as the curves suggest, but again this is a scale issue. Species occurrence can vary substantially among areas with different spatial patterns of snags and down wood, surrounding landscape conditions and site histories, and site conditions including presence of tree species and specific wood rot patterns. On a site level, tree species-specific rot patterns greatly influence wildlife species occurrence.

Incomplete Species Lists

No study provided data on all snag-associated species in any given habitat. Thus, the data tables and cumulative species curves in the wildlife component of DecAID provide only a partial insight into the full assemblage of wildlife (and fungi, cryptogams, and vascular plants, as well as invertebrates) that are associated with snags and down wood. In light of this incomplete knowledge, one might use a species rarefaction approach (e.g., James and Rathbun 1981, Palmer 1990, Tackaberry and others 1997) to estimate the full richness of species associated with snags and down wood, although there are potential problems associated with such an extrapolation. For now, we preferred to present just the empirical data.

Smoothing the Curves

The cumulative species curves jitter and bounce from vagaries in everything from sampling design to differences in specific habitat conditions at study sites. One could smooth the curves by using a lowess smoothing algorithm with an appropriate tension (weighting) value (e.g., 0.40) or some other smoothing function. We tested this but chose not to use this, so that the empirical data could be preserved in the curves, showing the conditions for each individual species or species group; smoothed curves would not provide species-specific information. Also, many curves for habitat types and structures not shown here are relatively data poor, and smoothing algorithms would not be appropriate in such cases.

Consider All Uses and Conditions

It is vital that all uses of snags or down wood, such as for breeding, feeding, and roosting, for given species be considered simultaneously when assessing impacts on species or when devising management guidelines. Considering only one type of wildlife use, especially a use that correlates with the smallest or fewest snags or down wood pieces, can prove insufficient to meet population needs.

DecAID and this wildlife component address terrestrial, upland conditions. Additional consideration needs to be made for snags and down wood in riparian, aquatic, and wetland environments.

The data and our synthesis do not explicitly represent some features of snags found to correlate well with some wildlife use. These data were entered into the master spreadsheet but have not been synthesized at this point. Such features include snag height and top condition (Raphael and White 1984). For some cavity-using birds and bats, snag height relative to live canopy height may be more critical than absolute height (Ormsbee, pers. comm.), and live foliage cover near snag cavities may provide important cover for birds (Nelson, pers. comm.).

Also, cautions need to be aimed at interpreting and using data from studies that spanned a variety of vegetation structures, treatments, or seral conditions. In a sense, each point for each species from such a study is a probability cloud itself representing variation among such conditions. Regressions or curves spanning different points may represent spurious relations. This is a major concern in meta-analysis methods of combining data from different studies. The best thing to do is be aware of the conditions in each reported study and interpret results accordingly.

Consider Other Decadence Elements

Some species select for decadence conditions not represented here, specifically hollow trees and logs, and dead parts of live trees. Such elements should be considered in addition to those presented here and will be included in DecAID. In many cases they may be rare enough to warrant complete protection where found, in coordination with health and safety standards.

Consider Use vs. Selection

Data based on patterns of selection (use compared with availability) should be interpreted differently than data based on occurrence or just use with no comparison to availability. Selection, as for particular sizes or densities of snags or down wood, when demonstrated, provides far greater evidence of what is needed to provide for wildlife. Still, use data can be applied to develop helpful guidelines for what to provide while selection studies get underway to test the guidelines.

Understanding the range over which snag or down wood sizes or densities were studied is also important. In some cases, there may appear to be no correlation or selection because more than adequate sizes or densities of snags or down wood were already provided, and the wildlife response had already leveled off.

Even if selection is demonstrated, some species may still be able to persist and even thrive if their preferred sizes or densities of snags or down wood were not available (e.g., Carey and others 1991). However, it is largely impossible to predict this for most species, and it may be prudent nonetheless to provide for sizes or densities according to the empirical selection studies.

Data on stand averages of snag or down wood density may or may not represent unmanaged conditions. Often, we could not determine this from the literature, so great care needs to be exercised when interpreting such data.

Population Response

The ultimate, and really the only authentic, measure of the effectiveness of snag and down wood management guidelines is how well they provide for fit, viable populations. Fitness is the reproductive vitality of offspring, and viability is the persistence of well-distributed populations over the long term. Few if any studies we reviewed truly measure fitness and viability. Thus, a major operating assumption is that wildlife (i.e., plant and animal) populations associated with snags and down wood would be fit and viable if 100 percent of all reported species' needs were met at the high statistical level. This can be empirically tested in large landscapes through an experimental approach, if desired, although such a study would be expensive and take many years. We encourage the reader to devise more tractable ways to model and test this critical assumption.

Under some conditions, populations of snag- and down wood-associated species may be limited by factors other than snag density, size, and condition. For example, based on a simulation model, Raphael (1983) suggested that, in Sierra Nevada mixed conifer forests, secondary cavity-nesting birds may be limited by territoriality rather than cavity abundance when snags are sufficiently numerous to provide nesting habitat for primary cavity-excavating species, at least for a time. His model then suggests that, in a burned forest with no further recruitment of snags, numbers of both primary cavity excavator species and secondary cavity-nesting species are limited by snag abundance as snag numbers decline beyond about year 20.

Remember Hardwoods

The data we gathered inadequately represent how hardwood trees provide for natural or excavated cavities for many species, such as for downy woodpecker *(Picoides pubescens)* and acorn woodpecker *(Melanerpes formicivorous)* in Westside Lowland Conifer/Hardwood Forests. Hardwoods would have to be added to the equation, particularly in forest types in which oaks, maples, and other broadleaf or hardwood species naturally occur.

Conclusions

We provide a new way to synthesize available scientific data on wildlife use of snags and down wood. This approach results in a series of “cumulative species curves” depicting low, moderate, and high statistical levels (means +/- SE or equivalent variant) of species’ use of snag density, snag size, down wood cover, and down wood size. This constitutes the wildlife component of the DecAID snag and down wood management advisory model. It provides an empirical and probabilistic “risk analysis” basis for determining snag and down wood management to meet wildlife management goals. It also provides a means of determining the degree to which wildlife species can be provided for a given density and size of snags and down wood by comparing to known use patterns from the literature. This approach provides a replicable framework by which to summarize existing studies, to integrate future studies, and to determine major information needs. The examples we present in this paper are but a small portion of all the literature we reviewed and analyzed *(appendix B).* Other publications (Marcot and others 2002) will provide the full set of analyses, cumulative species curves, management implications, and research guidelines.

Findings presented here also suggest that secondary cavity-using species associated with snags may use or select for greater snag numbers (or more locally dense snag clumps) and larger diameter snags than many of the primary cavity-excavating wildlife species. This suggests that the assumption used in previous models, that providing for primary species takes care of all species, may be invalid at least in some habitat types. This is also one example of how the wildlife component of DecAID can be used to generate testable working hypotheses for guiding future empirical research.

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Appendix A—*Species names and codes used in tables and figures.*

Species codes	Species names
ABBE	American black bear *(Ursus americanus)*
MAKE	American kestrel *(Falco sparverius)*
AMMA	American marten *(Martes americana)*
BBWO	Black-backed woodpecker *(Picoides arcticus)*[1]
BRCR	Brown creeper *(Certhia americana)*
BTWO	Bushy-tailed woodrat *(Neotoma cinerea)*
CBCH	Chestnut-backed chickadee *(Parus rufescens)*[1]
CLSA	Clouded salamander *(Aneides ferreus)*
CNB	Cavity nesting birds (unspecified species group)[1]
DEMO mammals	Several small mammal species included in the DEMO study
DOSQ	Douglas squirrel *(Tamiasciurus douglasii)*
DUSA	Dunn's salamander *(Plethodon dunni)*
ENSA	Ensatina *(Ensatina eschscholtzii)*
EUST	European starling *(Sturnus vulgaris)*
FUNG	Fungus spp. (unspecified species group)
GMGS	Golden-mantled ground squirrel *(Spermophilus lateralis)*
HAWO	Hairy woodpecker *(Picoides villosus)*[1]
HOWR	House wren *(Troglodytes aedon)*
LEWO	Lewis' woodpecker *(Melanerpes lewis)*[1]
MAPG	Mazama (western) pocket gopher *(Thomomys mazama)*
MASH	Marsh (Pacific Water) shrew *(Sorex bendirii)*
MOBL	Mountain bluebird *(Sialia currucoides)*
NFSQ	Northern flying squirrel *(Glaucomys sabrinus)*
NOFL	Northern flicker *(Colaptes auratus)*[1]
NOSA	Northwestern salamander *(Ambystoma gracile)*
NSOW	Northern spotted owl *(Strix occidentalis caurina)*
NTWO	Northern Three-toed Woodpecker *(Picoides tridactylus)*[1]
PCE	Primary cavity excavators (unspecified species group) [1]
PCFR	Pacific chorus frog, = Pacific treefrog *(Pseudacris regilla, = Hyla regilla)*
PGSA	Pacific giant salamander *(Dicamptodon tenebrosus)*
PIWO	Pileated woodpecker *(Dryocopus pileatus)*[1]
PJMO	Pacific jumping mouse *(Zapus trinotatus)*
PYOW	Northern pygmy-owl *(Glaucidium gnoma)*
RBNU	Red-breasted nuthatch *(Sitta canadensis)*[1]
RBSA	Red-breasted sapsucker *(Sphyrapicus ruber)*[1]
RONE	Rough-skinned newt *(Taricha granulosa)*
SCNB	Secondary cavity-nesting birds (unspecified species group)
SHMO	Shrew-mole *(Neurotrichus gibbsii)*
SMMA	Small mammals (unspecified species group)
SPFR	Spotted frog *(Rana pretiosa)*
SPSK	Spotted skunk *(Spilogale putorius)*
SRBV	Southern red-backed vole *(Clethrionomys gapperi)*
STWE	Shorttail weasel *(Mustela erminea)*
TOCH	Townsend's chipmunk *(Eutamias townsendi)*
TOVO	Townsend's vole *(Microtus townsendii)*

(*appendix A* continued)

Species code	**Species name**
TRSW	Tree swallow *(Iridoprocne bicolor)*
VASH	Vagrant shrew *(Sorex vagrans)*
WEBL	Western bluebird *(Sialia mexicana)*
WHHO	White-headed woodpecker *(Picoides albolarvatus)*[1]
WIWR	Winter wren *(Troglodytes troglodytes)*
WRSA	Western red-backed salamander *(Plethodon vehiculum)*

[1] Primary cavity-excavating species. All others are secondary cavity-using species or down wood-using species.

Appendix B—*The full set of habitat types and structures for which snag and down wood data have been synthesized for use in the wildlife component of the DecAID advisory model. The full data sets, table summaries, and confidence curves for snag and down wood amounts and sizes will be presented elsewhere.*

Parameter	**Habitat type**	**Habitat structure**	**Type of wildlife use**	**Examples given in this paper**
Snag density (no. snags per ha)	Eastside mixed conifer/ponderosa pine forest	post-fire	nesting/breeding	*table 1, figure 1*
	Eastside mixed conifer forest	forested	nesting/breeding and roosting/resting	
	Ponderosa pine forest	various	nesting/breeding and roosting/resting	
	Upland aspen forest	forested	nesting/breeding	
	Westside lowland conifer/hardwood forest	various	nesting/breeding	*table 1, figure 2*
	Westside lowland conifer/hardwood forest	clearcut plantations	nesting/breeding	
	Montane mixed conifer/lodgepole pine forest	various	roosting/denning	
Snag size (diameter)	Eastside mixed conifer/Ponderosa pine forest	post-fire	nesting/breeding	*table 2, figure 3*
	Eastside mixed conifer/ponderosa pine forest	various	foraging	
	Eastside mixed conifer forest	various	roosting/resting	
	Eastside mixed conifer forest	various (forested mosaic)	nesting/breeding	
	Ponderosa pine forest	various (forested mosaic)	nesting/breeding	
	Ponderosa pine forest	various	roosting/resting	
	Upland aspen forest	forested	nesting/breeding	

(*appendix B* continued)

Parameter	**Habitat type**	**Habitat structure**	**Type of wildlife use**	**Examples given in this paper**
Snag size (diameter)	Westside lowland conifer/hardwood forest	clearcut plantations	nesting/breeding	
	Westside lowland conifer/hardwood forest	various	nesting/breeding	*table 2, figure 4*
	Westside lowland conifer/hardwood forest	various forested	roosting/resting	
	Westside lowland conifer/hardwood forest	various	foraging	
	Lodgepole pine forests and woodlands	various	nesting/breeding	
	Lodgepole pine forests and woodlands	various	roosting/resting	
	Lodgepole pine forests and woodlands	various	foraging	
	Montane mixed conifer forest	various	nesting/breeding	
Down wood cover (percent)	Eastside mixed conifer forest	various	density and foraging	*table 3, figure 5*
	Southwest Oregon mixed conifer-deciduous forest	various	presence and nesting	
	Westside lowland conifer/hardwood forest	various	presence, abundance, and nesting	*table 3, figure 6*
	Lodgepole pine/subalpine fir forest	mature forest	nesting and density	
Down wood size (diameter)	Eastside mixed conifer/ponderosa pine	various	presence and foraging	*table 4, figure 7 (combined)*
	Westside lowland conifer/hardwood forest	various	presence and selection	*table 4, figure 7 (combined)*
	Lodgepole pine/montane forest	various	breeding and resting	

Demographics and Dynamics in Sierra Nevada Forests

Dead Branches and Other Wildlife Resources on California Black Oak (*Quercus kelloggii*)[1]

Barrett A. Garrison,[2] Robin L. Wachs,[3] Terry A. Giles,[4] and Matthew L. Triggs[5]

Abstract

In 1995, we began counting dead branches, mistletoe, and acorns on individually tagged living California black oak *(Quercus kelloggii)*. On the same plots, data on dead branches and mistletoe were recorded from ponderosa pine *(Pinus ponderosa)* in 1999. Number of dead branches per oak varied among the four stands ($P = 0.049$) and among the 5 years ($P < 0.001$). Large diameter oaks had more dead branches, acorns, and oak mistletoe *(Phoradendron villosum)* bunches ($P < 0.008$) than did small diameter oaks, while large diameter pines had more dead branches ($P < 0.001$) than did small diameter pines. In 1999, oaks averaged 1.33 dead branches per tree while pines averaged 0.45 dead branches per tree ($P < 0.001$), and 52 percent and 15 percent of oaks and pines, respectively, had dead branches ($P < 0.001$). Oak mistletoe was more prevalent in oaks (19 percent) than dwarf mistletoe *(Arceuthobium campylopodium)* was in pines (4 percent) ($P < 0.001$). Basal area of dead branches exceeded basal area of snags in the four stands. To some extent, dead branches can offset deficiencies in other forms of dead wood resources needed by wildlife.

Introduction

Dead wood in live trees is often overlooked by land managers when assessing dead wood resources of forest habitats. Because dead branches have value to wildlife (Powell and Zielinski 1994, Waters and others 1990), quantifying dead branch abundance should be useful when developing and implementing land management actions. Models for estimating snag densities required by woodpeckers have no

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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model components for dead branches that might provide cavities for primary and secondary cavity-nesting birds (Thomas and others 1979). Furthermore, some methods for determining snag densities do not include dead branches (Anonymous 1995, Bull and others 1990, Bull and others 1997, Morrison and others 1986a). Field inventories on National Forest lands include estimates of live crown-ratio and defects or decay of live trees but these are not explicit assessments of dead branch abundance (Anonymous 1995). In contrast, Chojnacky (1994) developed a method for estimating dead wood in live pinyon pines *(Pinus edulis)* and junipers (*Juniperus* spp.) because of decadence in these trees. Dead branches are a "hidden" resource that, if ignored, could bias management actions intended to correct deficits in snag abundance. Management actions taken to rectify perceived deficiencies in snag densities where trees are purposefully killed to create snags (Bull and others 1997, Chambers and others 1997, Lewis 1998) may be unnecessary or minimized in some cases if dead branches were quantified.

In mid-elevation mixed-conifer forests in the central Sierra Nevada where hardwoods and conifers occur, hardwoods provide important dead wood resources, such as dead branches, that may be lacking in conifers. California black oak is the dominant hardwood in these forests (McDonald 1988), and dead branches in living oaks are used by wildlife (Powell and Zielinski 1994, Waters and others 1990). Oaks also produce acorns that are important seasonal food for dozens of species of birds and mammals (Barrett 1980, Verner 1980). Leaves and berries of oak mistletoe, which occurs in California black oak, are eaten by many species of birds and mammals (Martin and others 1951). California black oaks grow differently, become decadent sooner, and have different snag characteristics[6] than do conifers (such as ponderosa pine), so they may provide substantially different dead wood resources in forests.

Initial field observations of the substantial amount of dead branches in living California black oak, lack of dead branches in conifers, and lack of management consideration for dead branch resources prompted us to undertake this study. Our objectives were to quantify dead branch abundance in California black oak; quantify abundance of other attributes in oaks that have wildlife values including acorn production and mistletoe infestation; compare dead branches and mistletoe infestations between California black oak and ponderosa pine to determine if these two species provide similar levels of these resources; and assess the relationship between tree diameter and abundance of dead branches, acorns (oaks only), and mistletoe.

Study Area

We worked on four 21.2-ha study stands in southern Placer County, California. The stands were similar in elevation and vegetation characteristics and were selected for a study of mule deer *(Odocoileus hemionus)* and other wildlife in oak-dominated habitat in the central Sierra Nevada (Garrison and others 1998a). Each stand consisted of two 10.6-ha subplots that were adjacent to each other. The paired subplots represented treatment and control units for an experimental timber harvest within each of the four stands that was conducted after this investigation. Elevations ranged from 1,240-1,450 m, and the stands were on plateaus and upper portions of

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[6] Unpublished data on file at California Department of Fish and Game, Sacramento Valley and Central Sierra Region, 1701 Nimbus Road, Suite A, Rancho Cordova, CA 95670.

steep river canyons. Study stands were located within large homogeneous forest stands with a tree layer dominated by large diameter (>40 cm diameter breast height) California black oak and ponderosa pine. Other less abundant tree species were interior live oak *(Q. wislizenii),* Douglas-fir *(Psuedotsuga menziesii),* white fir *(Abies concolor),* sugar pine *(P. lambertiana),* and incense cedar *(Calocedrus decurrens).* Seedling and sapling California black oak and ponderosa pine dominated the subcanopy at one stand, while the other stands had little subcanopy. The shrub layer was generally sparse, and deerbrush *(Ceanothus integerrimus)* and manzanita (*Arctostaphylos* spp.) were the most common shrubs. The herbaceous layer was dominated by sparse to dense cover of mountain misery *(Chamaebatia foliolosa).* Commercial timber harvesting of live conifers has occurred intermittently over the past several decades, and cutting of downed California black oak logs for fuelwood continuously occurs in all stands.

Methods

Each subplot occupied a 325-m x 325-m square area (10.6 ha) inside which we established a 250-m x 250-m sampling area (6.3 ha). The sample area was divided into a 25-m x 25-m grid with 11 stations per side (121 points in the grid), and a 37.5 m-wide buffer zone separated the sampling grid from the subplot boundary. All sampling occurred within the sampling grid. A total of 30 0.04-ha circular plots (15 circular plots per subplot) were randomly selected for vegetation measurements in each stand. In each subplot, 1 circular plot each was randomly selected in 1994 from the 11 points on each of the 11 alphabetized transects on the sampling grid, and 4 more circular plots were randomly selected from the same transects for each subplot in 1995. This resulted in a total of 15 circular plots per subplot and 30 circular plots per stand (2 subplots with 15 circular plot each per stand). Data from paired subplots were combined because subplots were adjacent to each other in the same stand. Vegetation sampling methods are described by Garrison and others (1998a), and data on live stems and snags were recorded using stem counts and diameter tapes. California black oaks were aged by counting annual growth rings from sections cut from trees harvested in 1998 and 1999.

A total of 32-36 individual California black oaks per stand were individually tagged in 1994 with numbered aluminum tags to assess acorn production. One tree ≥25 cm dbh was randomly selected from each 0.04-ha circular plot. An additional California black oak 13-25 cm dbh was tagged (2-6 per stand) whenever they occurred in the 0.04-ha plots to quantify acorn production by smaller, presumably younger, trees. In 1999, 30 individual ponderosa pines ≥13 cm dbh per stand were individually tagged from the 0.04-ha plots for comparisons between the two species. The tagged trees were the ones closest to the plot center stake. Diameters of all tagged trees were measured in 1994 (oaks) and 1999 (pines), using a diameter tape placed at a height of 1.37 m (dbh).

Beginning in 1995, we counted on each tagged tree the total number of dead branches that were ≥13 cm basal diameter (diameter at attachment to tree) and ≥0.7-m long from point of basal diameter to end. The 13-cm diameter threshold is the minimum required by some wildlife that use snags and dead branches (Bull and others 1997, Raphael and White 1984, Thomas and others 1979). We felt that 13 cm represented an appropriate size threshold as most branches had considerably greater diameters in oaks and approximately that diameter in pines.

Dead branches were identified by lack of bark, shredded bark, broken ends, and lack of live foliage. Counts included individual branches that fit the size criteria whether they were dead branches off dead branches or off live trunks and branches. Basal diameter did not include large, swollen bark wads growing at the base of the branch. Dead branches on the ground were measured with dbh tapes to calibrate visual measurements. Incidental observations were made of nesting cavities and other wildlife use.

Acorn production by California black oak was determined in late August-early September using visual counts of acorns in trees using methods of Garrison and others (1998b) and Koenig and others (1994a). The observer visually bisected the tree's live crown area into an upper and lower half, and all acorns observed during 15-second counts in each half were counted (total of 30 seconds). We also quantified infestation of California black oak by oak mistletoe and ponderosa pine by dwarf mistletoe by counting the number of mistletoe bunches in the tagged trees using binoculars (oaks) or noting mistletoe presence (pines). Mistletoe and acorns in live portions of the tree were counted during surveys for dead branches.

Total number of dead branches, acorns (oaks only), mistletoe bunches (oaks only) per tree were averaged among tagged oaks and pines within each stand and among years. Frequency of pines with dwarf mistletoe infestation was determined in lieu of counting mistletoe bunches because bunches were infrequently encountered (see below) and were more difficult to enumerate than oak mistletoe. Statistical comparisons for number of dead branches, acorns, and mistletoe bunches for California black oaks were made among stands and among years using a repeated measures analysis of variance (ANOVAs). Linear regression was used to determine linear relationships between California black oak diameter and average number of dead branches, acorns, and mistletoe bunches per tree over the 5-yr study. Linear regression was also used to determine the relationship between pine diameter and number of dead branches. Differences between number of dead branches for oaks and pines in 1999 were determined using t-tests. Differences between oaks and pines in frequency of trees with and without dead branches and mistletoe was determined using X^2 tests. Logarithmic ($\log_{10}$) transformations were applied to all variables used in the ANOVAs, t-tests, and regressions because the data had non-normal distributions (Zar 1996). All analyses were done using SYSTAT (Anonymous 1998), and statistical significance was set at $P < 0.05$.

Results

Stand Characteristics

Trunk diameters at the four stands for all live trees, hardwoods, and conifers $\geq$13 cm dbh averaged (quadratic mean) 39.4-53.9 cm, 37.4-63.5 cm, and 28.2-53.9 cm, respectively. Densities for all live trees, hardwoods, and conifers $\geq$13 cm averaged 190-326 trees/ha, 57-153 trees/ha, and 53-270 trees/ha, respectively. Basal area for all live trees, hardwoods, and conifers $\geq$13 cm averaged 30.5-43.2 m^2/ha, 7.3-21.6 m^2/ha, and 9.8-21.4 m^2/ha, respectively. Overstory canopy cover for all live trees, hardwoods, and conifers averaged 70.0-75.8 percent, 36.3-57.6 percent, and 12.9-33.7 percent, respectively. Height (m) for all live trees, hardwoods, and conifers averaged 15.8-22.4 m, 14.8-19.9 m, and 14.9-26.5 m, respectively. Age of California black oaks (n=10 for each stand) in the stands averaged 120-166 yrs (age range of individual trees 53-347 yrs) (Garrison and others 2002).

California Black Oak Attributes

Number of dead branches per tree in California black oak varied among stands ($F_{3,134}$ = 2.69, P = 0.049) and years ($F_{4,536}$ = 5.13, P < 0.001) *(table 1).* There was significant interaction between stands and years ($F_{12,536}$ = 2.52, P < 0.004) as some stands had consistently more dead branches per tree during all years. Wildlife observed in our stands foraging, nesting, or roosting in dead branches included northern pygmy-owls *(Glaucidium gnoma),* downy woodpeckers *(Picoides pubescens),* mountain chickadees *(Poecile gambeli),* red-breasted *(Sitta canadensis)* and white-breasted *(S. carolinensis)* nuthatches, and brown creepers *(Certhia americana).*[7] Mistletoe bunches per tree in California black oak varied among stands ($F_{3,134}$ = 5.43, P < 0.002), and there was no variation among years ($F_{4,536}$ = 2.08, P = 0.091) nor any significant stand by year interaction ($F_{12,536}$ = 1.26, P = 0.240) *(table 1).* Acorn production per tree varied among stands ($F_{3,134}$ = 10.60, P < 0.001) and years ($F_{4,536}$ = 54.96, P < 0.001) *(table 1).* There was significant interaction between stands and years ($F_{12,536}$ = 12.88, P < 0.001) as some years (1995 and 1999) and stands (two and four) produced more acorns than others. Larger diameter oaks had more dead branches per tree than smaller diameter oaks ($R^2_{adj.}$ = 0.586, n = 138, $t_{(2)}$ = 13.87, P < 0.001) *(fig. 1).* Larger diameter oaks also produced more acorns per tree ($R^2_{adj.}$ = 0.051, n = 138, $t_{(2)}$ = 2.69, P = 0.008) and had more mistletoe bunches per tree ($R^2_{adj.}$ = 0.125, n = 138, $t_{(2)}$ = 4.41, P < 0.001) than smaller diameter oaks, although the relationships were not as strong as with dead branches because many trees did not have mistletoe or produce acorns *(fig. 1).*

Table 1—*Mean ± SD for number of dead branches >13 cm diameter, mistletoe bunches* (Phoradendron villosum), *and number of acorns/30 seconds per tree for California black oaks* (Quercus kelloggii) *from four 21.2-ha stands from 1994-1999, Placer County, California.*[1]

Attribute	Stands	n	1995	1996	1997	1998	1999	All years
Dead branches	1	32	2.06±2.45	1.69±2.65	1.41±1.79	1.63±2.09	1.91±2.10	1.74±0.25
	2	36	1.75±2.18	0.75±1.13	0.94±1.51	0.72±1.39	1.53±1.89	1.14±0.40
	3	36	1.31±1.70	1.64±2.10	1.06±1.79	1.00±1.27	1.08±1.30	1.22±0.26
	4	34	0.68±1.04	0.65±0.88	0.47±0.83	0.79±1.37	0.62±1.05	0.64±0.12
	All	138	1.44±1.96	1.17±1.86	0.96±1.55	1.02±1.57	1.28±1.68	1.17±0.20
Mistletoe	1	32	0.59±1.64	1.28±3.90	0.72±2.26	0.63±1.90	1.09±2.56	0.86±0.31
	2	36	1.58±3.51	2.25±5.54	2.06±4.76	1.89±3.98	2.25±4.66	2.01±0.28
	3	36	0.42±1.23	0.89±1.92	0.75±2.06	0.81±1.79	0.50±1.52	0.67±0.20
	4	34	0.00±0.00	0.03±0.17	0.03±0.17	0.00±0.00	0.00±0.00	0.01±0.02
	All	138	0.66±2.12	1.12±3.59	0.91±2.93	0.85±2.48	0.97±2.89	0.90±0.17
Acorns	1	32	2.09±3.77	0.00±0.00	0.03±0.18	0.00±0.00	0.16±0.72	0.46±0.92
	2	36	4.39±9.16	0.67±2.10	0.00±0.00	1.11±3.46	16.11±20.74	4.46±6.73
	3	36	5.50±14.53	0.08±0.37	0.00±0.00	0.00±0.00	1.33±3.96	1.38±2.37
	4	34	10.24±16.07	0.12±0.41	0.18±0.63	0.06±0.24	1.12±3.42	2.34±4.44
	All	138	5.59±12.22	0.23±1.13	0.05±0.33	0.30±1.82	4.86±12.73	2.21±2.77

[1] See text for statistical differences among stands and years; data from 2 10.6-ha subplots within each stand.

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[7] Unpublished data on file at California Department of Fish and Game, Sacramento Valley and Central Sierra Region, 1701 Nimbus Road, Suite A, Rancho Cordova, CA 95670.

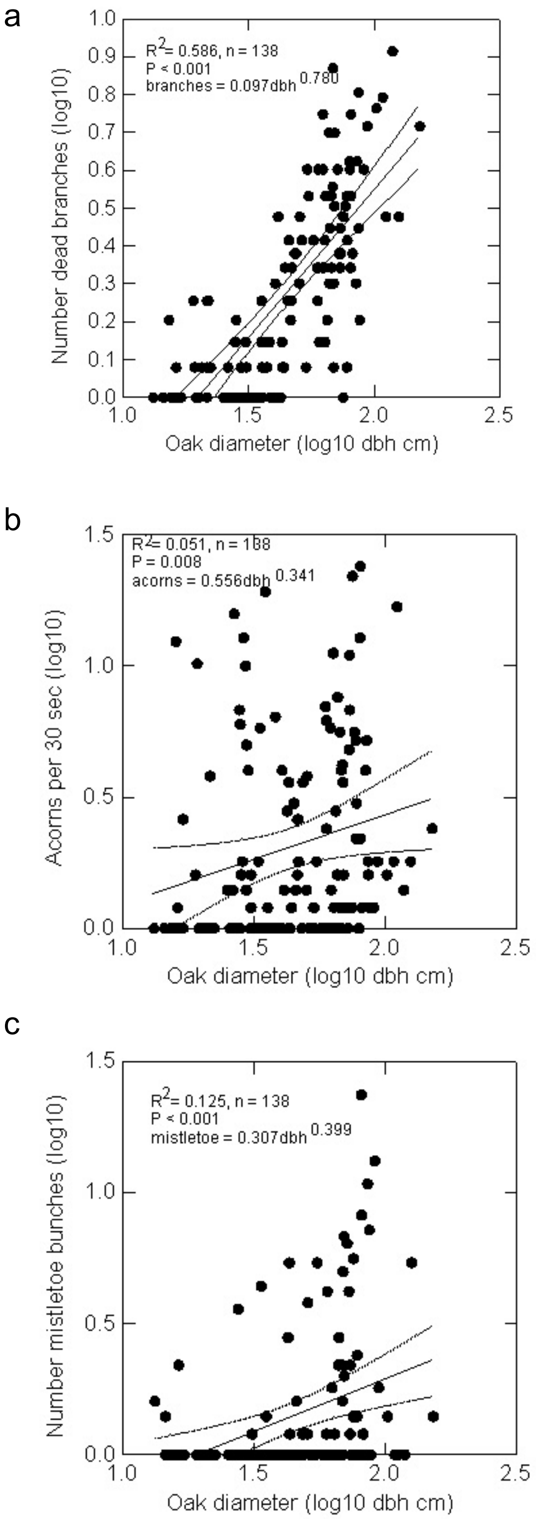

Figure 1—Relationships between stem diameter of California black oak *(Quercus kelloggii)* ($\log_{10}$ dbh cm) and (a) average number of dead branches ($\log_{10}$) per tree, (b) average number of acorns/30 seconds ($\log_{10}$) per tree, and (c) average number of mistletoe bunches *(Phoradendron villosum)* ($\log_{10}$) per tree.

California black oak and ponderosa pine had equivalent stem diameters ($t_{(2)}$ = -1.72, df = 241.3, P = 0.868), but oaks had almost three times more dead branches than pines ($t_{(1)}$ = 5.92, df = 259.0, $P < 0.001$) *(table 2).* Dead branches were found in 52 percent of oaks and 15 percent of pines (X^2 = 39.45, df = 1, $P < 0.001$). Mistletoe was found in 19 percent of oaks and 4 percent of pines (X^2 = 13.97, df = 1, P = 0.0002). Larger diameter pines had more dead branches than smaller diameter trees ($R^2_{\text{adj.}}$ = 0.261, n = 120, $t_{(2)}$ = 6.46, $P < 0.001$, dead branches = $0.338 * \text{dbh}^{0.420}$), but the relationship was not as strong as with oaks.

Table 2—*Mean ± SD (min, max) for several characteristics per tree of California black oak* (Quercus kelloggii) *and ponderosa pine* (Pinus ponderosa) *measured in 1999 at four 21.2-ha stands in Placer County, California.*[1]

Characteristic	California black oak (n=144)	Ponderosa pine (n=120)	P-values from tests[2]
DBH (cm)	51.15±27.09 (13.2, 152.0)	60.67±36.89 (15.0, 188.8)	0.087
Dead branches ≥13 cm diameter	1.33± 1.72 (0.0, 8.0)	0.45± 1.30 (0.0, 8.0)	0.001
Pct trees with dead branches ≥13 cm diameter	52.1 pct	15.0 pct	0.001
Number of mistletoe bunches[3]	0.98± 2.86 (0.0, 23.0)	—	—
Pct trees with mistletoe[2]	19.4 pct	4.2 pct	0.001

[1] Data from two 10.6-ha subplots within each of the four stands.

[2] T-tests for dbh and dead branch numbers and X^2 for frequency of trees with dead branches and mistletoe.

[3] Oak mistletoe *(Phoradendron villosum)* in California black oak and dwarf mistletoe *(Arceuthobium campylopodium)* in ponderosa pine.

Discussion

California black oaks had dead branches with diameters ranging from a few cm to large branches >30 cm, while ponderosa pines had dead branches mostly at the 13-cm diameter threshold. Larger diameter (>40 cm) oaks and pines had more dead branches than smaller diameter oaks and pines, but this relationship was stronger with oaks. California black oak acorn production and mistletoe infestation were variously distributed among stem diameters. There were many oaks without dead branches (30 percent) or mistletoe (48 percent) and that did not produce acorns (38 percent), showing that all trees do not provide these resources.

Because amounts of dead branches, acorns, and mistletoe in California black oak varied by stand and individual tree, there were localized differences in abundance of these resources. Stands had some differences in elevation, aspect, slope, age, and vegetative characteristics, so some variation could be explained by stand differences. Individual trees, however, likely accounted for most differences, as tree dbh explained 59 percent of the variance in dead branch number, while stand amounts were barely significantly different (P = 0.049). Oak dbh explained only 13 percent and 5 percent of the variance in mistletoe bunches and acorns, respectively, because many trees of all diameters lacked acorns or mistletoe. Conversely, amounts of mistletoe and acorns varied ($P < 0.002$) among stands, so individual tree characteristics were less important than stand attributes. Stand-level differences were most pronounced with mistletoe and acorns compared to dead branches.

Numbers of dead branches and acorns from California black oak varied annually, although there were no obvious increasing or decreasing trends. Dead branch abundance varies as branches fall off and trees are damaged due to storms (Matlack and others 1993, Webb 1989). Observer differences (Block and others 1987) also may have caused some variation. Annual variation occurs in acorn production by California black oak due to spring weather conditions (Koenig and others 1994b). Annual variation occurs in ponderosa pine cone production (McDonald 1992), and nuts from cones also are eaten by wildlife (Martin and others 1951). Although we did not measure cone production, we feel the two tree species provide equivalent food resources to wildlife. Oaks, however, had greater numbers of dead branches and more mistletoe than the pines. Dwarf mistletoe in ponderosa pine is also food for wildlife (Martin and others 1951). Therefore, live California black oaks and ponderosa pines provide multiple resources to wildlife in our study stands. Ponderosa pines, however, have less dead branch and mistletoe resources than do California black oaks.

In some areas, management efforts may be necessary to increase snag numbers (Chambers and others 1997, Lewis 1998, Morrison and others 1986b, Thomas and others 1979), but these efforts may be unnecessary in habitats with large numbers of larger diameter California black oak. Managers should quantify dead branch resources in live California black oaks and other trees, and snag abundance should be combined with dead branch abundance to fully quantify the amount of standing dead wood. Basal area of all snags, including hardwoods and conifers, in our study areas averaged 2.34 m^2/ha, and that amount was relatively low compared to snag abundances reported from spotted owl *(Strix occidentalis)* habitat in the Sierra Nevada (Gutierrez and others 1992) and other locations in the Sierra Nevada (Morrison and others 1986a).

Increasing snag levels in our stands through directed management might be justified based on snag basal area alone, but might not be necessary when dead branches are considered with other dead wood resources. For example, using grand means from the four stands for the number of dead branches per oak (1.17 dead branches/tree) and the number of living oaks per ha (113 oaks $\geq$13 cm dbh/ha), there were 2,803 dead branches $\geq$13 cm diameter in each 21.2-ha study stand. In the four study stands, there were 11,211 dead branches $\geq$13 cm diameter from California black oak. Oak dead branch basal area averaged 1.72 m^2/ha with 13-cm diameters, and dead branch basal area is certainly greater in the stands because many dead branches were >13 cm diameter.

Using similar calculations for ponderosa pine, which averaged 0.45 dead branches/tree in 1999, there were 1,336 dead branches $\geq$13 cm diameter in each 21.2-ha study stand, 5,344 dead branches $\geq$13 cm diameter in the four study stands, and an average of 0.82 m^2/ha of dead pine branch basal area. Total snag basal area in our stands was 2.34 m^2/ha, while total dead branch basal area for California black oak and ponderosa pine was 2.54 m^2/ha. While not all dead branches are useful to wildlife, particularly smaller diameter branches (Bull and others 1997, Thomas and others 1979), we observed many being used by several species of birds for nesting, roosting, and feeding. Our limited field observations indicated that wildlife used some dead branches of oaks but did not use dead branches of pines.

Management of forest and woodland habitats is shifting from traditional methods emphasizing single species and individual resources (e.g., snags, acorns, etc.) to communities and ecosystems (Chapel and others 1992, Hunter 1990). Forest ecosystems are diverse, and ecosystem management efforts require assessments of the presence and/or abundance of many habitat attributes. Dead branches are often overlooked during these assessments, and our study has shown that these resources can be substantial in certain habitats and particular locations. With shorter lengths and mostly smaller diameters, dead branches cannot fully duplicate the total dead wood volume of many snags, particularly conifers, which provide very tall snags. Yet, we observed that dead branches were used by wildlife, and dead branches were more numerous and had greater cross-sectional area than snags.

Variation in dead branches, mistletoe, and acorns among locations and years indicates that assessments should be conducted at multiple locations and over many years to adequately measure amounts of these resources. In some instances, cavities in live and dead trees and branches may not limit populations of cavity-nesting birds (Waters and others 1990), so managers should inventory snags and dead branches prior to initiating management efforts to increase dead wood abundance. Furthermore, where snag abundances are particularly low due to fuel woodcutting efforts, dead branches may replace or offset snag losses. Dead branches were more prevalent in large diameter oaks, so trees must be allowed to grow old enough to provide dead branches of appropriate diameters for wildlife use. Large diameter trees also are the oldest oaks in the stand (Garrison and others 2002), so forest management should retain these trees as well as replace them as they die. Because California black oaks are intolerant to shade and respond favorably to canopy openings, individual tree, small group selection, or thinning harvests that open canopies, reduce competition from conifers, retain older and larger oaks, and recruit young oaks through stump sprouting and acorn germination are appropriate management actions (McDonald 1969, Tappeiner and McDonald 1980).

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Demography of Snags in Eastside Pine Forests of California[1]

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Abstract

Nine years of annual observations of snags on 24, 5-hectare plots in northeast California were analyzed. *Pinus ponderosa, Pinus jeffreyi*, and *Abies concolor* were the most abundant tree species. The rate and timing of snag creation varied between species. Of the snags standing at the end of the observation period, 88 percent retained their original height; 6 percent of the *Pinus jeffreyi* and 12 percent of the *Abies concolor* were rendered generally unsuitable for cavity nesting birds by height loss; and 13 percent of the *Pinus jeffreyi* and 4 percent of the *Abies concolor* lost bark cover during the observation period. On an annual basis, 7 percent of the pine snags and four percent of the *Abies concolor* snags fell over. The "half life" for snags was 6 years for the pine species and 8 years for *Abies concolor*. Increases in snag fall rate occurred after prescribed fire. The total amount of snags increased during the observation period.

Introduction

The benefits and costs of snags and their derivatives have been well documented (Bull and others 1997, Dudley 1982, Maser and Sedell 1994, Valdez 1996, Weatherspoon and Skinner 1996). However, information about the rates at which snags are created, accumulate, decay, and ultimately fall down is scant. This information is useful when making inferences about habitat quality, productivity, fire hazard, and human safety, all important components of ecosystem health. It is also useful when planning and predicting levels of snags across a landscape through time.

Two major studies of snag dynamics have been reported from California. Keen (1955) summarized 30 years of annual surveys of beetle-killed ponderosa pine *(Pinus ponderosa)* from five 256-ha plots in northeastern California and southern Oregon. That study had the advantage of a relatively long observation period and of knowing when individual trees died, but was limited to pure ponderosa pine killed by one agent. Raphael and Morrison (1987) summarized observations on four species from eight 8.5 hectare plots installed over a 4-year period and re-measured 5 years later on the eastern slope of the Sierra Nevada near Truckee. That study included several agents of tree mortality, several tree species, and some site variation, but was limited

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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by a relatively short observation period and by not knowing when individual trees died.

This paper uses data from an ongoing study from annual surveys over a 9-year period from 24, 5-hectare plots within the Modoc Plateau and Southern Cascade ecological sections (McNab and Avers 1994). It includes several agents of mortality, several species, and relatively broad site variation, but is limited by not knowing when snags in the initial observation died and the relatively short observation period to date. Large sample sizes of ponderosa pine (*Pinus ponderosa*, PP), Jeffrey pine (*Pinus jeffreyi*, JP*),* and white fir (*Abies concolo*, WF) are included. Small sample sizes of western juniper (*Juniperus occidentalis*, WJ), lodgepole pine (*Pinus contorta*, LP), incense cedar (*Calocedrus decurrens*, IC), black oak (*Quercus californica*, BO), and red fir (*Abies magnifica*, RF) are included. The silvical characteristics of these species have been documented (Burns and Honkala 1990). Many factors contribute to rates of creation, decay, inventory, and fall, including soil characteristics, topographic position, climate, stand density, incidence of root disease, windstorms, and firestorms, amount of decay before death, time since death, species, diameter, and the proportion of heartwood. The purpose of this paper is to provide information on snag demographics and associated variation with tree species, diameter, time since death, and fire history, for improving predictions of future condition and for planning and implementing landscape and larger scale projects.

Methods

Twenty-four sites were selected from a pool of about 2,000 mapped polygons, segmented into six density classes. Each site is 5 hectares in size (500m by 100m). The sites were established at selected locations in 1988 and 1989.

Site Characteristics

The sites are within either the Modoc Plateau or Southern Cascade ecological sections on either the Modoc National Forest, the Lassen National Forest, the Blacks Mountain Experimental Forest, or the Lassen Volcanic National Park.

These sites are characterized by long dry summers. Mean annual temperature ranges from 7 to 11 ºC. Mean annual precipitation ranges from 300 to 760 mm. *Table 1* summarizes site characteristics. These sites exist across a range of temperature and moisture. Some sites (Baseball, Four-mile, Pease Cabin, Pease Flat) only support ponderosa pine and western juniper. They are relatively warm-dry sites. Other sites (Butte Lk 1, Butte Lk 2, Lost Creek 3) support red fir. They are relatively cold-moist sites. Still others (Bieber, Pit River) support California black oak. They are relatively warm-moist sites. Most sites are relatively cool and moist and support Jeffrey pine, ponderosa pine, and white fir in some combination. White fir exists on the edge of its range in some of these sites as limited by available water and is relatively more abundant now than earlier in the century.

Over the 9-year period of observation wildfire, prescribed fire, harvest, or some combination of the three have occurred on some, but not on most, sites *(table 1).*

Table 1—*Numbers of snags on each of the 24, 5-ha study sites.*

Site	Wildfire	Rx Fire	Harvest	JP	PP	WF	WJ	LP	IC	BO	RF	Total[1]
Ashurst				9	37	67						113
Baseball					66		12					78
Bieber				17	1		2		2	6		28
BM34/125		Fall 1997	1996	1	52							53
BM34/151b			1997	36	55	215						306
BM34/151				73	93	63						229
BM34/75		Fall 1997	1996	10	55							65
BM34/ Roseburg		Fall 1997		41	106	68						215
BM34/Snags		Fall 1997	1996	8	59							67
BM34/ Squirrel			1997	61	47	109			4			221
BM35/88			1996	118	48	53			5			224
Butte Lk 1		1990 & 1995		155	32	47					1	235
Butte Lk 2				128	13	20					4	165
Butte Lk 4				220		9		35				264
Four-mile					133		39					172
Lost Creek 1		Spring 1999		150	3	3		15			2	173
Lost Creek 3				458		11						469
N Mud Lake	1996			1	13							14
Pease Cabin					17		4					21
Pease Flat					125		8					133
Pit River				18	18	265	4		32	2		339
Soup Creek				65	3	9	1					78
S Mud Lake				6	20		14					40
Whitehorse				24	3	5						32
Grand Total				1,599	999	944	84	50	43	8	7	3,734

[1] These snag counts reflect total individual snags that have been observed. The counts disclosed elsewhere will not match these totals for various reasons. Twenty snags have no recorded diameters; 90 snags were consumed or felled by fire; 349 snags were harvested; 13 snags on the Baseball site have been topped at 30 or 40 feet to lower the risk of blow-down and promote decay from the top. Individual snags come into and out of analysis depending on the question being examined.

Data Collection

All snags present in the year of establishment were mapped and individually marked. Trees were considered snags when all needles were dead. Jeffrey pine and ponderosa pine snags were often hard to distinguish in the field. Species, diameter, height, and percent bark cover on the bole were recorded. Year of death for these snags is not known. Sites have been resampled with the same protocol each year since establishment. New snags were added to the record (year of death is known). Status of previously measured snags (standing or down), new height, new percent bark cover, and effects of fire or cutting were recorded.

Analysis

Creation Rates

Creation rates were established for Jeffrey pine, ponderosa pine, and white fir by tallying the number of snags that entered the study in each of the years 1990 through 1998 *(table 2)*. To compare the patterns of drought and snag creation, annual averages of monthly values for the Palmer Drought Severity Index were compiled from National Climatic Data Center's State Division 2 data, which includes the Sacramento Valley and Modoc Plateau.

Table 2—*Percent and count by year of snags still standing since death.*

Year of death	Years since death								
	0	1	2	3	4	5	6	7	8
Ponderosa pine	**Percent of snags still standing, by years since death**								
1990	100	97	97	90	82	66	53	50	48
1991	100	98	92	80	61	46	43	39	
1992	100	96	91	80	54	48	46		
1993	100	100	91	72	67	60			
1994	100	100	92	86	83				
1995	100	98	93	86					
1996	100	98	95						
1997	100	94							
Average		98	93	83	69	55	47	45	48
Keen's Avg		100	97	93	89	85	73	58	50
Ponderosa pine	**Count of snags still standing, by years since death**								
1990	62	60	60	56	51	41	33	31	30
1991	61	60	56	49	37	28	26	24	
1992	82	79	75	66	44	39	38		
1993	58	58	53	42	39	35			
1994	36	36	33	31	30				
1995	43	42	40	37					
1996	57	56	54						
1997	34	32							
1998	10								
Jeffrey pine	**Count of snags, by years since death**								
1990	49	48	45	36	33	26	18	17	18
1991	50	49	45	41	38	29	23	23	
1992	33	32	32	28	27	27	22		
1993	91	88	81	73	70	65			
1994	131	128	117	108	104				
1995	216	209	201	197					
1996	138	137	133						
1997	94	94							
1998	17								

(*table 2* continued)

Year of death	Years since death								
	0	1	2	3	4	5	6	7	8
White fir	**Count of snags, by years since death**								
1990	20	17	17	11	11	10	7	7	9
1991	36	36	36	34	30	28	28	32	
1992	39	39	39	39	37	33	35		
1993	89	89	88	88	86	80			
1994	56	55	55	54	54				
1995	256	251	241	227					
1996	76	72	71						
1997	32	31							
1998	43								

Inventory

Inventory equals initial count plus creation minus fall. The inventory of snags through time was calculated for each of four diameter classes (13 + cm, 13-36 cm, 38-74 cm, and 76 + cm diameter at breast height) for Jeffrey pine, ponderosa pine, and white fir.

Decay Rates

Decay rates were inferred from reductions in percent bark cover and height.

Fall Rates

Fall rates were calculated three ways. First, a value was obtained for each year of observation by dividing the number of fallen snags by the total at the beginning of the year, then those yearly values were averaged over the years of observation. We call this the average annual fall rate. Source data for this calculation is provided in *table 3*. The equation is

$$\frac{\sum\left(\frac{Number\,Falling_i}{Number\,at\,Beginning_i}X100\right)}{n}$$

in which:

i = population based on observation year
n = number of populations

Table 3—*Average annual snag fall rates by species and diameters.*

Year	1989	1990	1991	1992	1993	1994	1995	1996	1997
	Jeffrey pine–all diameters								
Initial count	657	698	692	699	711	787	929	984	1,023
Number that fell	8	56	26	79	55	84	83	57	38
Fall rate for the year	1.2 pct	8.0 pct	3.8 pct	11.3 pct	7.7 pct	10.7 pct	8.9 pct	5.8 pct	3.7 pct
Avg. annual fall rate	6.8 pct								
	Jeffrey pine–13-36 cm								
Initial count	335	363	347	350	338	364	423	455	472
Number that fell	5	41	13	47	35	54	51	34	21
Fall rate for the year	1.5 pct	11.3 pct	3.7 pct	13.4 pct	10.4 pct	14.8 pct	12.1 pct	7.5 pct	4.4 pct
Avg. annual fall rate	8.8 pct								
	Jeffrey pine–38-74 cm								
Initial count	224	234	242	239	254	288	338	365	384
Number that fell	3	14	9	22	17	16	23	19	17
Fall rate for the year	1.3 pct	6.0 pct	3.7 pct	9.2 pct	6.7 pct	5.6 pct	6.8 pct	5.2 pct	4.4 pct
Avg. annual fall rate	5.4 pct								
	Jeffrey pine–76+ cm								
Initial count	98	101	103	110	116	132	165	162	164
Number that fell	0	1	4	10	3	4	8	4	0
Fall rate for the year	0.0 pct	1.0 pct	3.9 pct	9.1 pct	2.6 pct	3.0 pct	4.8 pct	2.5 pct	0.0 pct
Avg. annual fall rate	3.0 pct								
	Ponderosa pine–all diameters								
Initial count	411	467	510	575	600	579	555	531	528
Number that fell	6	18	17	33	57	67	81	37	26
Fall rate for the year	1.5 pct	3.9 pct	3.3 pct	5.7 pct	9.5 pct	11.6 pct	14.6 pct	7.0 pct	4.9 pct
Avg. annual fall rate	6.9 pct								
	Ponderosa pine–13-36 cm								
Initial count	161	183	201	244	250	222	207	198	201
Number that fell	2	11	11	23	36	47	46	18	17
Fall rate for the year	1.2 pct	6.0 pct	5.5 pct	9.4 pct	14.4 pct	21.2 pct	22.2 pct	9.1 pct	8.5 pct
Avg. annual fall rate	10.8 pct								
	Ponderosa pine–38-74 cm								
Initial count	131	150	163	171	185	199	191	183	184
Number that fell	1	5	4	6	8	13	21	8	7
Fall rate for the year	0.8 pct	3.3 pct	2.5 pct	3.5 pct	4.3 pct	6.5 pct	11.0 pct	4.4 pct	3.8 pct
Avg. annual fall rate	4.5 pct								
	Ponderosa pine–76+ cm								
Initial count	118	133	145	159	165	158	156	149	142
Number that fell	3	2	2	3	13	7	14	11	2
Fall rate for the year	2.5 pct	1.5 pct	1.4 pct	1.9 pct	7.9 pct	4.4 pct	9.0 pct	7.4 pct	1.4 pct
Avg. annual fall rate	4.2 pct								
	White fir–all diameters								
Initial count	142	161	193	226	299	345	580	636	645
Number that fell	1	4	6	16	10	21	21	23	19
Fall rate for the year	0.7 pct	2.5 pct	3.1 pct	7.1 pct	3.3 pct	6.1 pct	3.6 pct	3.6 pct	2.9 pct
Avg. annual fall rate	3.7 pct								

(*table 3* continued)

Year	1989	1990	1991	1992	1993	1994	1995	1996	1997
	White fir–13-36 cm								
Initial count	48	63	87	105	151	163	370	411	415
Number that fell	0	3	3	10	7	11	17	18	12
Fall rate for the year	0.0 pct	4.8 pct	3.4 pct	9.5 pct	4.6 pct	6.7 pct	4.6 pct	4.4 pct	2.9 pct
Avg. annual fall rate	4.6 pct								
	White fir–38-74 cm								
Initial count	57	62	68	84	110	140	166	181	187
Number that fell	0	1	2	5	3	6	2	4	6
Fall rate for the year	0.0 pct	1.6 pct	2.9 pct	6.0 pct	2.7 pct	4.3 pct	1.2 pct	2.2 pct	3.2 pct
Avg. annual fall rate	2.7 pct								
	White fir–76+ cm								
Initial count	37	36	38	37	38	42	44	44	43
Number that fell	1	0	1	1	0	4	2	1	1
Fall rate for the year	2.7 pct	0.0 pct	2.6 pct	2.7 pct	0.0 pct	9.5 pct	4.5 pct	2.3 pct	2.3 pct
Avg. annual fall rate	3.0 pct								
	Western juniper–all diameters								
Initial count	66	66	69	68	68	69	69	70	69
Number that fell	0	1	2	1	1	2	5	2	0
Fall rate for the year	0.0 pct	1.5 pct	2.9 pct	1.5 pct	1.5 pct	2.9 pct	7.2 pct	2.9 pct	0.0 pct
Avg. annual fall rate	2.3 pct								
	Western juniper–13-36 cm								
Initial count	60	60	61	60	60	61	61	61	60
Number that fell	0	1	2	1	1	2	5	2	0
Fall rate for the year	0.0 pct	1.7 pct	3.3 pct	1.7 pct	1.7 pct	3.3 pct	8.2 pct	3.3 pct	0.0 pct
Avg. annual fall rate	2.6 pct								
	Lodgepole pine–all diameters								
Initial count	30	30	34	38	35	36	34	30	36
Number that fell	0	0	1	4	0	2	4	1	0
Fall rate for the year	0	0	2.9 pct	10.5 pct	0.0 pct	5.6 pct	11.8 pct	3.3 pct	0.0 pct
Avg. annual fall rate	0.0379								
	Incense cedar–all diameters								
Initial count	27	27	29	30	31	30	36	36	38
Number that fell	0	0	0	0	1	0	3	3	1
Fall rate for the year	0.0 pct	0.0 pct	0.0 pct	0.0 pct	3.2 pct	0.0 pct	8.3 pct	8.3 pct	2.6 pct
Avg. annual fall rate	2.5 pct								

Second, the number of years it took for half the snags to fall was calculated. We call this the half-life. Snags initially tallied in different years were assigned to separate populations. Half-lives were calculated separately for each population. Populations where more than a 50 percent decline occurred were included. The average value for included populations is reported. Source data for this calculation is provided in *table 4*. The equation is

$$\frac{\sum \left(Time\, it\, Takes\, for\, Half\, the\, Snags\, to\, Fall_i \right)}{n}$$

in which:

i = population based on year of death
n = number of populations

Third, the display used in Keen (1955) *(table 5, fig. 1)* of percent of snags still standing by years since death was duplicated for comparison (ponderosa pine only).

Table 4—*Half-life of snags by tree species and diameters.*

Snag counts										
	Observation year									
Population year	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**
	Jeffrey pine–all diameters									
1989	679	671	616	596	529	484	431	374	347	330
1990		55	54	51	42	39	31	21	20	18
1991			51	50	46	42	38	29	23	23
1992				35	34	34	30	29	27	22
	Jeffrey pine–13-36 cm									
1989	347	342	302	294	256	227	186	155	142	134
1990		36	35	33	26	23	19	12	11	12
1991			26	25	22	20	18	14	11	11
1992				18	17	17	15	15	13	8
	Jeffrey pine–38-74 cm									
1989	231	228	214	206	186	173	165	148	137	128
1990		16	16	15	14	14	10	8	8	5
1991			22	22	21	19	17	12	9	9
	Ponderosa pine–all diameters									
1989	471	465	449	434	413	372	341	305	273	225
1990		64	62	62	58	53	43	35	33	31
1991			79	78	74	67	55	36	28	24
1992				111	108	104	95	58	44	38
1993					68	67	62	51	43	37
	Ponderosa pine–13-36 cm									
1989	170	168	159	148	132	105	85	73	63	53
1990		25	23	23	21	17	12	8	8	7
1991			45	45	43	40	31	15	9	6
1992				78	75	73	65	36	23	20
1993					35	35	30	23	17	14

(*table 4* continued)

Snag counts

Population year	**Observation year** **1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**
	Ponderosa pine–38-74 cm									
1989	160	159	154	151	148	143	137	125	114	96
1990		21	21	21	19	19	16	13	11	11
1991			18	17	16	13	10	8	7	7
1992				16	16	16	15	10	9	7
	White fir–all diameters									
1989	187	186	185	179	169	161	147	130	128	87
1990		30	27	27	21	21	20	17	17	7
1991			56	56	56	54	50	47	47	26
	White fir–13-36 cm									
1989	64	64	64	61	57	51	44	38	38	21
1990		24	21	21	15	15	14	11	11	2
1991			39	39	39	38	35	34	34	21
	White fir–38-74 cm									
1989	71	71	70	68	63	61	58	54	53	40
	Western juniper–all diameters									
1989	65	65	64	62	60	59	57	52	50	50
	Lodgepole pine–all diameters									
1989	30	30	30	29	25	25	23	20	19	19
	Incense cedar–all diameters									
1989	27	27	27	27	27	26	26	24	24	24

Table 5—*Changes in snag height between 1989 and 1997.*

	All snags		**Jeffrey pine**		**White fir**	
	Count	**pct**	**Count**	**pct**	**Count**	**pct**
No height change	2,007	88	892	90	547	86
New height under 6 meters	165	7	55	6	75	12
New height over 6 meters	107	5	49	5	14	2
Total	2,279		996		636	
Started over 6 meters and changed	275					
New height is under 6 meters tall	151	55				

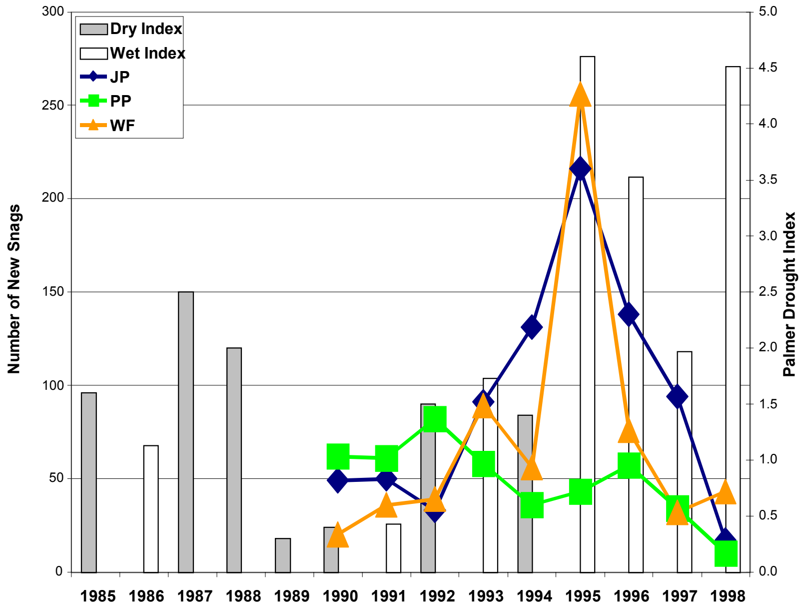

Figure 1—Numbers of new snags and the Palmer Drought Severity Index.

Results

Creation Rates

Ponderosa pine snags were created on a generally declining trend ranging from 82 to 10 total new snags on all study sites combined per year. White fir increased from 20 new snags per year to 256 in the spike year of 1995, then declined to 43 new snags in 1998. Jeffrey pine ranged from 33 new snags per year to 216 in the spike year of 1995, then declined to 17 new snags in 1998 *(table 2)*. The early part of the period was relatively dry; the latter part was relatively wet *(fig. 1)*.

Inventory

Total snag levels generally increased during the first 6 years then leveled off. Small white fir increased the most. Ponderosa pine exhibited a different pattern than Jeffrey pine and white fir *(table 3; fig. 2)*.

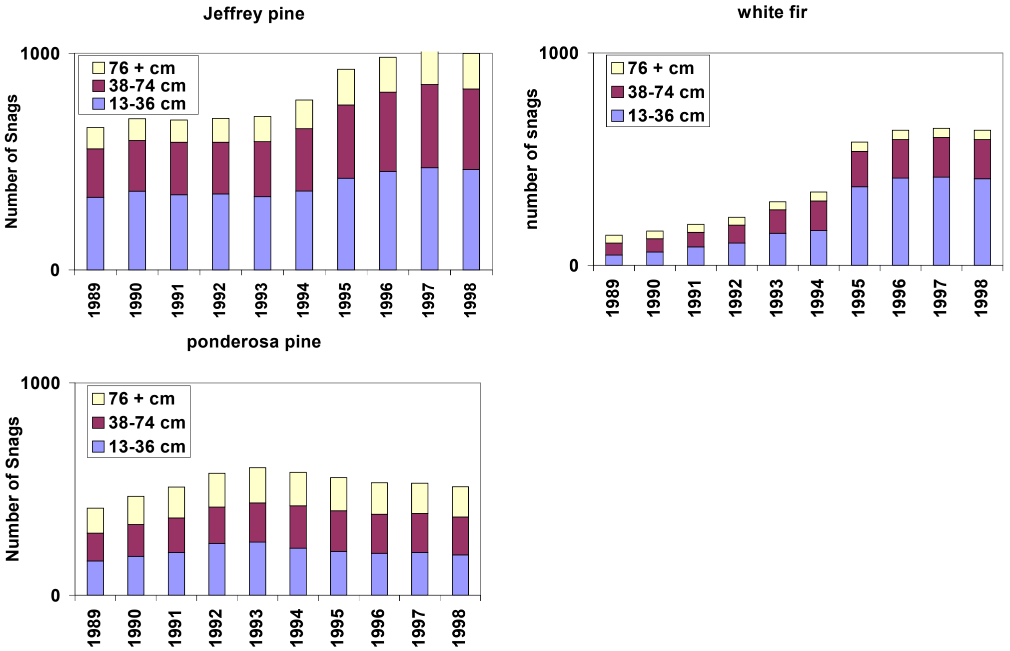

Figure 2—Numbers of snags of the three dominant tree species existing on all study sites from 1989 through 1998.

Decay Rates

Records for snags that were topped, cut, burned, or have no diameter recorded were not included in the analysis of decay rates, and only snags that were standing in 1998 were included.

For those snags standing in 1998, 88 percent retained their height during the period of observation *(table 5)*. Ninety percent of the Jeffrey pine and 86 percent of the white fir retained their height. Six percent of the Jeffrey pine and 12 percent of the white fir have new heights under 6 meters, which is considered a general suitability threshold for cavity nesting birds. This suggests that white fir tend to break off more frequently while Jeffrey pine tend to fall over. For those Jeffrey pines that did have height reduction, the average height changed from 20 meters to 7 meters. For those white firs that did have height reduction, the average height changed from 17 to 4 meters. About half (55 percent) the snags tall enough to function as cavity nesting habitat became unsuitable (under 6 meters tall).

Over the 9 years, very few snags lost bark cover. Only 4 percent of the white fir and 13 percent of the Jeffrey pine lost bark cover *(table 6)*. Among Jeffrey pine where bark cover change occurred, average bark cover changed from 89 percent to 54 percent. The corresponding change for white fir was from 99 percent to 84 percent.

Table 6—*Changes in percent bark cover.*

	All species		Jeffrey pine		White fir	
	Count	pct	Count	pct	Count	pct
No change	1,945	85	870	87	612	96
Changed	334	15	126	13	24	4
Total	2,279		996		636	

Fall Rates

Annual fall rates of snags varied by diameter and species *(table 7)*. Fall rates were greater for smaller diameter classes; for the pine species the largest diameter classes fall rates were less than half of the smallest diameter class. Both pine species had greater fall rates than the non-pines.

Snag half-life, the time required for 1/2 of the snags to fall, was less for the pine species compared to the other tree species. Western juniper snag half-lives were about twice as great as the pines *(table 8)*.

Table 7—*Average annual fall rate of snags.*

	Diameter class			
Species	All	13-36cm	38-74cm	76cm+
JP	6.8 pct	8.8 pct	5.4 pct	3.0 pct
PP	6.9 pct	10.8 pct	4.5 pct	4.2 pct
WF	3.7 pct	4.6 pct	2.7 pct	3.0 pct
WJ	2.3 pct	2.6 pct	-	-
LP	3.8 pct	-	-	-
IC	2.5 pct	-	-	-
BO	-	-	-	-
RF	-	-	-	-

Table 8—*Half-life of snags (in years).*

	Diameter Class			
Species	All	13-36 cm	38-74 cm	76 cm+
JP	6	6	7	-
PP	6	5	8	-
WF	8	7	10[1]	-
WJ	17[1]	-[2]	-	-
LP	11[1]	-	-	-
IC	-	-	-	-
BO	-	-	-	-
RF	-	-	-	-

[1] These values are outside the range of observation. They are linear trendline estimates.

[2] - Not enough observations to warrant a meaningful calculation.

Comparison with Keen (1955)

Fall rates for ponderosa pine in this study are a little more rapid than Keen reported for pure ponderosa pine observed earlier this century *(fig. 3)*. Half-life in this study is about 6 years compared to about 8 years reported by Keen (1955). Some difference should be expected due to different average diameter, 46 cm in this study compared to 61 cm reported by Keen (1955).

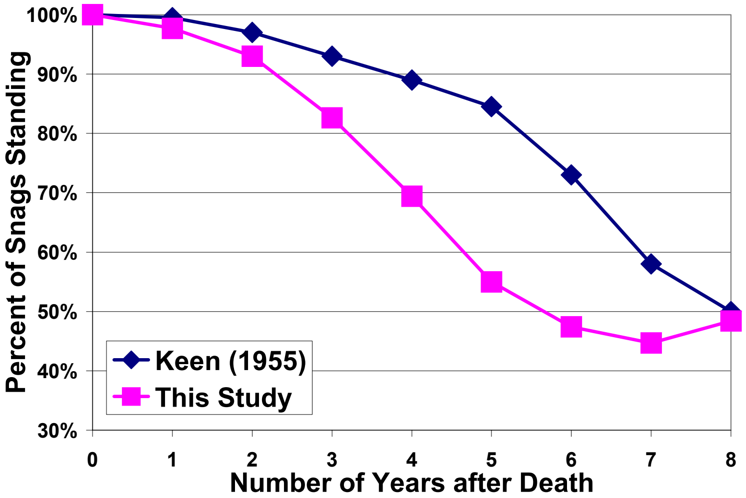

Figure 3—Losses of snags through time comparing Keen's (1955) results with those reported here.

The Influence of Fire

Site BM34/Roseburg, was prescribe-burned after snag observations in the fall of 1997. Including records for snags consumed or felled by fire, the average annual fall rate (all species and diameters combined) for the eight periods prior to the burn was 3 percent compared to the 20 percent rate that occurred after the burn *(table 9)*.

Table 9—*The influence of Rx fire on snag fall rate.*

Species	'89-'90	'90-'91	'91-'92	'92-'93	'93-'94	'94-'95	'95-'96	'96-'97	'97-'98
JP/PP/WF	0 pct	0 pct	0 pct	3 pct	2 pct	7 pct	9 pct	4 pct	20 pct

Three sites, BM34/125t, BM34/75Ti, and BM34Snag, were thinned and harvested in 1996 and Rx burned in 1997. By eliminating the harvested trees from the data, the influence of fire can be inferred. The average annual fall rate (all species and diameters combined) for the eight periods prior to the burn was 8 percent compared to the 19 percent rate that occurred after the burn *(table 10)*.

Table 10—*The influence of Rx fire on snag fall rate.*

Species	'89-'90	'90-'91	'91-'92	'92-'93	'93-'94	'94-'95	'95-'96	'96-'97	'97-'98
JP/PP	3 pct	3 pct	1 pct	4 pct	13 pct	7 pct	21 pct	15 pct	19 pct

The Influence of Wildfire and Harvest

Both wildfire and harvest have affected some of the study sites. Virtually all trees on the N Mud Lake site have been killed by wildfire; only 12 snags remain on the 5-hectare site. Several of the sites within Blacks Mountain Experimental Forest have been harvested as part of a long-term research project. The consequence of harvest on fall rate can obviously range from insignificant to highly significant.

Discussion

These results should help people predict decay rates and fall rates for snags at the landscape and larger scale through time. Variation in these rates may be high, so cautious application is warranted and incorporation of variation as an objective is suggested. Silvicultural prescriptions designed to provide specified levels of snags by species and size over specified timeframes should also be informed by this study.

Creation Rates

The variation in rate of snag creation between tree species and between size classes within a species is not readily explained. More analysis is needed to gain insight in this regard. Among other factors, the density of green trees on these study sites is not known. Density can accelerate the formation of snags, especially during drought. Host specific insects and diseases may also cause different patterns of creation.

Decay Rates

The fact that 85 percent to 96 percent of the snags standing in 1998 have had no change in height or bark cover over the period of observation is not surprising, because many snags are new during the study period and those that existed initially are relatively stable. We expect significantly more top breakage and bark loss over the next 10 years.

The relative differences in decay rates between Jeffrey pine and white fir are hard to evaluate because the number of years since death is not known for many of the snags. What appears to be faster decay in Jeffrey pine may be simply a result of older age. Many of the pine initially tagged in 1989 were killed by bark beetles in the late 1970s.

The fact that, of those trees experiencing height loss, about half end up under 6 meters tall, has significant habitat implications for some cavity dependent species. The fall rates disclosed here underestimate the snag habitat loss rates that occurred because snags of any height were included.

Fall Rates

A presumed negative exponential fall rate is not indicated in this data, probably because the observation period is too short to reflect one. Keen (1955) and Everett and others (In Press) both report a negative exponential form—one from long term observations and one from a chronosequence of wildfires.

The influence of tree species on fall rate was expected. Average annual fall rates of about 7 percent for ponderosa pine/Jeffrey pine, 4 percent for white fir/lodgepole pine, 3 percent for incense cedar, and 2 percent for western juniper seem appropriate in the absence of fire for mid-term planning at landscape and larger scales. More time is needed to verify an exponential rate for longer term planning.

The influence of tree size on fall rate was generally expected. For ponderosa pine/Jeffrey pine, average annual fall rates of about 10 percent for smaller snags, 5 percent for medium sized snags, and 4 percent for large snags were observed. The reader is cautioned that understanding the calculation method is important when interpreting these results. As used here, annual fall rate is the number of snags falling in a given year expressed as a percentage of snags that were present at the beginning of the year. Each year stands on its own. The calculation is made separately each year.

The influence of fire is significant. Prescribed burning significantly increases snag fall rates for at least 1-year after the fire occurs. Plans that include periodic prescribed burns should combine average annual fall rates with periodic increased rates during burn years.

The effect of site variables such as micro-climate, soil, slope position, disease, and disturbance history have not been adequately examined but are expected to influence both decay rate and fall rate.

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Assessing the Effect of Fire Regime on Coarse Woody Debris[1]

Pamela Wright,[2] Mark Harmon,[3] and Fred Swanson[4]

Abstract

This study used field data and modeling to examine how coarse woody debris (CWD) differs between two areas that experienced different fire regimes (120- to 300-year mean fire return intervals) in the 1500-1850 period. Although fire frequency and severity established the overall pattern of CWD succession, the interaction of fire regime with other controlling factors caused the differences in CWD mass at the landscape scale. CWD mass was almost twice as high in landscapes having an infrequent, stand-replacing fire regime (173 Mg/ha) as in landscapes having a moderately frequent, mixed-severity fire regime (95 Mg/ha). Factors that appear to have the greatest influence are decomposition rates, fire severity, fire frequency, and fuel consumption, suggesting that environment and stand structure—together with fire regime—are more important than fire regime alone. CWD levels have greater temporal variability in the infrequent, stand-replacing fire regime than in the mixed-severity regime, primarily because of the different timing of mortality.

Introduction

Although a few studies have examined the relationship between coarse woody debris (CWD) and natural disturbance, particularly fire, they have primarily examined the most simple, stand-replacing fires in which all trees are killed and no subsequent fire occurs for several hundred years. Studies and syntheses by Agee and Huff (1987), Harmon and others (1986), and Spies and others (1988) depict the succession of CWD conditions after fire. During a stand-replacing fire, large amounts of biomass are converted from live to dead matter. While some biomass is consumed in a fire, much more is converted from live to dead and is carried into the subsequent stand. CWD is therefore highest just after such a fire. This material persists as the regenerating stand develops and usually is the dominant source until the live trees begin to provide woody debris of a large size. As the pulse from the fire begins to decompose, CWD in the stand decreases, reaching its lowest level in the mature

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stand. CWD rises again in late succession as mortality from the regenerated stand increases. It levels off when mortality and decomposition reach a "steady-state."

Although this simple pattern occurs in many areas, more complex fire regimes with multiple fires during the life of a stand, which kill only some trees, are also common. The purpose of this paper is to examine the effect of fire regime on CWD amounts. Specifically, we asked: 1) Do the CWD levels differ among two fire regimes? 2) How are CWD levels affected by fire severity and frequency? and 3) How do the other factors that control CWD vary by fire regime?

To answer these questions, we contrasted two regimes in the west Central Oregon Cascades that were distinguished in fire history studies on the basis of fire frequency and severity (Connelly and Kertis 1992, Morrison and Swanson 1990, Teensma 1987). One regime had infrequent, high-severity fires. The mean fire return interval was more than 300 years, and the oldest trees—more than 450 years old—originated from stand-replacing fires that occurred during drought periods in the 1500s. This regime occurred in cool, moist environments, such as north-facing slopes and headwaters. Fires in this regime created large patch sizes of single-aged stands. The second regime exhibited more frequent, mixed-severity fires. Here, the fire severity ranged from low to high, creating a mosaic of small patches with multiple disturbance cohorts of shade tolerant tree species within single stands. The mean fire return interval was 95 to 150 years with a mean of about 120 years. Some trees survive these fires, but the oldest trees were usually just 200 years old. This regime occurred on south-facing slopes and south-facing drainages.

Our first step was to develop a conceptual model of how CWD was affected by different fire regimes. The second step was to collect data on trees, snags, and downed logs, in areas with both fire regimes. Third, we developed a simple model that simulated the pattern of CWD mass after fire and did a comparative analysis of field data and model results. We then used the model to understand how fire frequency and severity, stand growth and development, decomposition and mortality rates, and fuel consumption may have affected the CWD levels observed in the field, and to investigate how each of these factors may have affected the CWD mass in the two regimes.

Study Area

The study was conducted on the Willamette National Forest near the town of Blue River, in the Central Oregon Cascades. Two areas were sampled that are 35 km apart and lie north and south of the McKenzie River in the Willamette Basin. The study area has long, wet winters and relatively dry, warm summers, typical of the west side of the Oregon Cascades and Coast Range. The average annual temperature is 9.5°C at 430 m elevation, and precipitation is 2,400 mm per year with more than 70 percent falling from November through March. The sampled stands are primarily within the Western Hemlock Forest Vegetation Zone (670-1,067 m), although some upper elevation plots fell in the ecotone between the Western Hemlock Zone and the adjacent Pacific Silver Fir Zone (1,067-1,676 m) (Franklin and Dyrness 1988). Field sampling included all parts of the moisture and temperature gradients in the Western Hemlock Zone, although it did not include all conditions found in the central Cascade Mountains described by Zobel and others (1976) *(fig. 1).*

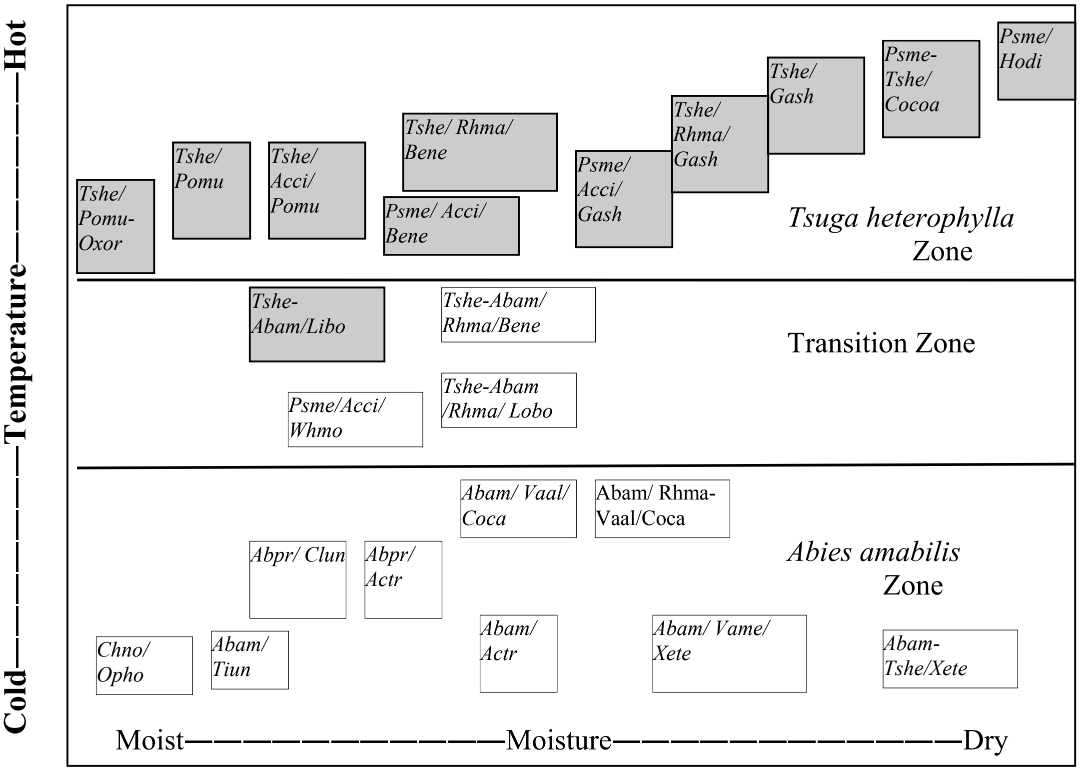

Figure 1—Vegetation along temperature and moisture gradients for the central western Cascade Mountain Range (Dyrness and others 1974, Zobel and others 1976). Shaded boxes are plant associations sampled in the study area.

Field Sampling

The study area was stratified by fire regimes defined by other studies and stands were sampled in two areas for each of the two fire regimes described above. Field sampling included an inventory of a total of 57 stands ranging in size from about 50 to 150 ha. Stands were delineated on aerial photos to sample the full range of stand ages, elevations, and aspects, and to sample the extent of the area identified by the fire history studies. Within each stand five randomly selected variable-radius plots were sampled.

At each plot, information was recorded about physical conditions such as percent slope, aspect (degrees azimuth), topographic position, plant association (Hemstrom and others 1987), and elevation (m). In each stand, variable radius plots were used to sample live trees. Diameter at breast height (DBH) of each tree tallied >23 cm was recorded to convert basal area to stem count per ha (Dilworth and Bell 1985).

To estimate the mass of downed CWD, we sampled logs >23 cm in diameter at the point of intersection (Brown 1974, Van Wagner 1968) with two perpendicular transects intersecting at plot center 100 m in total length (50 m up and downhill, 50 m along contour). Diameters of logs were measured, and species and decay class were recorded according to a classification system widely used in the Pacific Northwest (Fogel and others 1973, Sollins 1982, Triska and Cromack 1980).

Snags were measured in an 800 m^2 belt transect. Snags >23 cm diameter and greater than 0.5 m tall were measured at breast height and recorded by species, diameter, height, and a decay class scheme developed by Cline and others (1980) similar to the log decay classification scheme. Heights were estimated visually after the heights of a few snags on each transect were measured with a clinometer and tape.

To compare mortality rates for the areas having different fire regimes, we calculated the ratio of CWD volume by decay class to live tree volume, and estimated the volume of CWD that accumulated each year. We calculated the total CWD volume in each decay class and estimated the length of time the trees had been dead, using rough estimates of residence time in each decay class. To estimate the average mortality rate for each fire regime for the past 2 centuries, we averaged the rates for all decay classes in the four sampling areas. The mortality rate was calculated as:

$$\textit{Mortality Rate year}^{-1} = (\textit{CWD Volume/Live Tree Volume})/\textit{Residence Time year}^{-1}.$$

in which *CWD Volume* is the total *CWD volume* by decay class for each sampling area, *Live Tree Volume* is the mean tree volume for stands in each sampling area, and *Residence Time* is the number of years CWD remains in each decay class.

This assumes live tree volume is static through time, which is probably only true for older stands when tree volume levels off. Residence time for Douglas-fir log decay classes are comparable to other studies, and since it dominated species composition, it was used to estimate the mortality rate for field data. Residence time was estimated by assuming CWD remains in Decay Class 1 for 15 years, in Class 2 for 15-44 years, in Class 3 for 45-89 years, in Class 4 for 90-145 years, and in Class 5 for 150-225 years.

Statistical Analysis

We performed a randomized block, two-way analysis of variance (ANOVA) and paired t-test with the two geographic sites (north of the McKenzie River and south of the McKenzie River) as blocks to determine if the CWD mass in the two fire regimes varied significantly at a p-value < 0.10. (SAS Institute, Inc. 1992). We also performed a Chi-squared test to determine whether the distribution of CWD among the decomposition classes differed significantly between the two fire regimes.

A paired t-test was used to determine whether site productivity of the sampling areas with different fire regimes varied significantly. Using the plant associations identified in the field, we compared site indices (height of a Douglas-fir in 100 years from McArdle and others 1961) and performed a paired t-test at a p-value of 0.10 to determine if the differences in mean site indices were statistically significant between the two regimes.

Model Description

We constructed a simulation model, FIRECWD, based on the conceptual model developed by Harmon and others (1986), which considers the store of CWD in an ecosystem and how it changes through time. The model accounts for the CWD that is input to the system by mortality (e.g., fire events, bark beetles, or root rot), the amount that is lost (e.g., decomposition and consumption by fire), and the levels of CWD mass that result.

The purpose of the model was to simulate CWD dynamics for the two fire regimes, compare the mean and standard deviation of CWD between modeled and field estimates, and gain insights into the behavior of the system by changing input and control variables. The model was built to run in Microsoft Excel or Quatro Pro for Windows 5.0,[5] and used to explore the effects of fire frequency, fire severity, site productivity, decomposition, mortality, stand growth, and fuel consumption on CWD succession.

A full description of the model can be found in Wright (1998). A general description follows. This model expresses the essential elements of vegetation and fuel succession using the body of knowledge from previous research. A stochastic element allows the model to simulate the variability that might be expected for CWD. FIRECWD randomly selects years in which fire occurs within the limits that reflect the fire regime, such as once every 200 years or once every 500 years. It is programmed to simulate the natural variation expected in maximum biomass, decomposition and mortality rates, growth parameters, and pre-fire CWD.

Live Biomass

The live biomass function simulates tree growth and biomass that accumulates in the stand between fires. In the years when fires occur, a portion of the trees are killed and live biomass representing that portion is converted to CWD mass, while a small portion is consumed by the fire. The amount of the conversion depends on fire severity. The portion of the live biomass remaining continues to grow, and live biomass continues to accumulate from the level it was reduced by the fire. In the case of the stand-replacing fire regime, the live biomass would be reduced 85 percent +/- 15 percent, and for a mixed-severity fire regime, it would be reduced 50 percent +/- 15 percent. For example, in the stand-replacing fire regime, the live biomass begins accumulating from an average 15 percent of the live biomass existing in the year of the fire.

The total live biomass of trees was estimated from stand age, a Richards function parameterized with the maximum live biomass the site can support, the time to reach the maximum biomass, and a parameter that controls the point of inflection (Richards 1959). The maximum biomass was estimated from site index based on plant associations and a growth and yield model, DFSIM (Curtis and others 1982). DFSIM output indicated that a site with average productivity in the study area at a stand age of 300 years would have a live biomass of about 700 Mg/ha.

Fire Disturbance

This part of the model is used to simulate the direct effects of fire on CWD mass. In the year when a fire occurs, the pulse input of CWD mass created by a fire depends on the total live biomass currently in the system and the fire severity. Fires occur stochastically based on a probability estimated from the fire return interval for a site. To simulate randomly occurring fires, a spreadsheet cell indicating fire

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[5] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

occurrence is linked to a column in which a random number is produced for each annual time step. If this random number is greater than the annual probability of fire, a fire occurs. This allows the model to simulate the fire frequency and severity of a regime, such that severity is greater when time intervals between fires are longer.

Fuel Consumption

This part of the model calculates the mass of CWD lost due to fuel consumption. The model also tracks the portion of CWD stores that are not reduced by fuel consumption. Fuel consumption, estimated from previous research, is assumed to average 20 +/- 5 percent of the total CWD mass already present in the year of the fire, and 5 percent of the live biomass converted to CWD mass by the fire (Brown and others 1985, Reinhardt and others 1991).

Non-fire Mortality

This part of the model is used to simulate the CWD mass that accumulates from chronic mortality in the new stand from factors such as stem exclusion, insects, pathogens, and wind. We assume that as the new stand grows, 0.005 per year of the live tree biomass dies. This amount varies randomly +/- 0.00125 per year for each model run. For the first 50 years after a fire, trees are quite small (diameters <10 cm) and not considered CWD. The dead trees that accumulate after the fiftieth year are considered CWD mass.

Decomposition

This part of the model is used to simulate the decomposition of CWD mass. For any given year, the total CWD mass has three sources: fire created CWD, old CWD, and CWD created by non-fire mortality. The decomposition function is applied to all three sources calculating the mass of CWD lost from decomposition. The average decomposition rate constant for the ecosystem is assumed to be 0.020+/- 0.005 per year.

Randomization

The model is stochastic with each simulation run producing a slightly different output. Consequently, the model can generate “data” to test effects of different fire regimes and control variables using statistics. Each run generally parallels the mean value, but individual runs can be quite a bit higher or lower than the mean depending on the parameter values selected. To vary the parameters between model runs, we created one cell in the spreadsheet for the mean value and one for the standard deviation for each parameter, and two associated cells with random numbers. One specifies how much to deviate the parameter, and another indicates whether the deviation is added to or subtracted from the mean value. We divided this uniform distribution into unequal segments so that its frequency distribution took on the form of a normal distribution.

Results

Coarse Woody Debris Mass

The field measurements of CWD indicate that on average stands with the mixed-severity fire regime had about half as much CWD as sites with the stand-replacing fire regime *(table 1)*. However, an ANOVA and a paired t-test revealed no statistically significant difference ($p < 0.29$) in total CWD mass between the two regimes.

Table 1—*Mean, standard deviation, and range of CWD mass for field data for each regime individually and sites combined by regime.*

			CWD mass (Mg/ha)		
Fire regime	**Sample area**	**Number of stands**	**Mean**	**Standard deviation**	**Range**
Stand-replacing	Lookout	12	190	99	100-420
	Augusta	15	155	105	55-411
	Combined	27	173	102	55-420
Mixed-severity	Cook-Quentin	14	73	40	30-155
	Chucksney	16	115	72	18-258
	Combined	30	95	56	18-258

The model predicted a more similar CWD mass between the two regimes than did the field data *(table 2)*. The model results also indicated less variability in CWD mass within the fire regimes than the field data. These model results indicated that fire frequency and severity alone are probably not responsible for the different amounts of CWD mass found in the field data and that site productivity, decomposition and mortality rates, and/or stand growth may also control CWD mass differences in the areas with different fire regimes.

Table 2—*Mean, standard deviation, and range of CWD mass (Mg/ha) from model data varying all the control factors within the expected range for two fire regimes. Control factors include fire-killed biomass, decomposition rate, mortality rate, maximum biomass, and B1 and B2 in the growth function. Range is the mean minimum and maximum for 30 model runs.*

		-----------CWD mass (Mg/ha)----------		
Fire regime	**Mean fire return interval**	**Mean**	**Standard deviation**	**Range**
Stand-replacing	300	212	28	133 - 807
Mixed-severity	125	188	39	102 - 571

Site Productivity

Field results of the site indices in the study area overlap considerably. The mode of site indices in the study area was 136, and the stands experiencing a stand-replacing fire regime had only a slightly higher mean site index than stands with the mixed-severity fire regime (135 vs. 132). A paired t-test indicated that site productivity was not different statistically ($p < 0.80$).

The site indices for the study area span only a small range of the possible values for site index, and consequently the effect of site productivity on differences in CWD mass between the fire regimes is not significant. Sensitivity analysis indicates that the model is highly responsive to this factor. Within the area we sampled, however, site productivity probably plays a minor role in controlling the different levels of CWD mass found in the two fire regimes because site index is fairly constant.

Tree Biomass

Tree biomass measured in the field showed that stands with the stand-replacing fire regime had 100 Mg/ha more mass than the average of the stands in the mixed-severity fire regime (752 and 649 Mg/ha respectively). The stands with a stand-replacing regime are older (100-450 years) than stands with a mixed-severity regime (90-150 years), and older stands would be expected to have greater tree biomass than younger stands. The model has low sensitivity to the parameters that influence the amount of time necessary for the stand to become established and the time period required for mean annual growth to level off. Varying these parameters has little effect on differences in CWD mass. Accordingly, these growth, rate-related parameters have little effect on CWD over time, and they probably also have little influence on the different levels of CWD between the two fire regimes.

Mortality

The mortality rates from the field data for the two fire regimes indicate that the non-fire mortality rate (i.e., suppression mortality, disease, wind, etc.) is only slightly different between the areas having different fire regimes. The model has an intermediate level of sensitivity to mortality, but varying the mortality rate within the expected range had little effect on the total CWD mass. The combined results from the field data and the modeling indicate mortality is a relatively unimportant factor in explaining the difference in total CWD accumulation between the areas having two fire regimes.

Decomposition

Sensitivity analysis indicates that the model is highly responsive to changes in the decomposition rate constant. Previous research efforts indicate that a high degree of variation exists in decomposition rate estimates (Harmon and others 1986, Sollins 1982, Spies and others 1988). Varying the decomposition rate within the range found in the west central Oregon Cascade Mountains results in considerable differences in CWD mass over time. Decomposition rate appears to have the greatest effect on CWD of all control factors examined. For example, increasing the decomposition rate to 0.050 year^{-1} would reduce CWD mass to less than one-third the mass that would be present if the decomposition rate were 0.010 year^{-1} *(table 3).*

Table 3—*Modeled mean CWD mass (Mg/ha) averaged more than 500 years for the two fire regimes for decay rates 0.01 to 0.05 from 30 model runs for each regime.*

Decomposition rate constant	Stand-replacing 300 yr. MFRI	Mixed-severity 125 yr. MFRI
0.010	387	319
0.020	212	188
0.030	153	133
0.040	127	112
0.050	111	96

Fuel Consumption

Although there are no field data for fuel consumption (the study area has been free of fire for decades), we used the model to estimate the effect of fuel consumption on CWD mass for the two regimes. The model has a low sensitivity to fuel consumption, but model runs of randomly occurring fires indicate that the effect of fuel consumption from fires in the mixed-severity regime would be considerably higher than for the stand-replacing fire regime because more fires occurred (4 fires vs. 1.6 fires per 500-year period). Results indicate that even with this reduction from fuel consumption, the mass indicated by the model (206 and 167 Mg/ha) is still considerably higher than the CWD field data (173 and 96 Mg/ha).

Fire Killed Biomass

Using live tree biomass observed in the field as an estimate of potential CWD input from fires and using model data (which indicates low sensitivity), it appears that fire-caused mortality has a large effect on CWD mass for the first 100 years after a fire, but then the effect rapidly diminishes. This is because decomposition is an exponential function and reduces fire-created CWD mass rapidly the first years after a fire. The analysis also indicates that a much longer time period is necessary for CWD to recover in a stand-replacing regime (more than 200 years) than in a mixed-severity regime (about 100 years).

Discussion

CWD Mass in the Two Fire Regimes

Field data indicated that CWD mass is consistently higher across the stands in the stand-replacing regime, with an average CWD mass almost twice as high as the stands in the mixed-severity regime. Although the differences were not statistically significant, due to high variability, there are readily apparent differences in CWD mass *(table 1).* Furthermore, no recently burned stands were sampled, and therefore, stands with high mass created by such fires were not considered. Given that stand-replacing fires initially input a higher dead wood mass, one would expect the differences between regimes might be even greater. Trends may have been even more pronounced had the field study included areas where fire regimes are more dissimilar than those found in the western Cascades of Oregon.

Fire suppression probably did not influence the field results greatly; however, in areas with the mixed-severity regime it may have some implications for future development of CWD. Over the last 50 to 70 years the effects of wildfire on the landscape have been minor, and much biomass is now tied up in small live trees. Therefore, a wildfire now would probably be more severe than typical for this regime because of the high numbers of small, suppressed trees. The fire-created CWD would then be more similar to that occurring in a stand-replacing regime, including a larger pulse and a much longer recovery time.

Model Uncertainty

Model predictions are uncertain for two reasons: 1) the model's sensitivity to parameters, and 2) the observed variation in parameters. If a model is not sensitive to a parameter, that parameter probably does not greatly influence uncertainty. In contrast, if a model is sensitive to a parameter and its value does not vary, then uncertainty is low. If the model is sensitive to a parameter and its value varies widely, however, it can introduce major uncertainty to the analysis. For example, modeled CWD mass is not especially sensitive to fire frequency and severity, and since the regimes are clearly defined in terms of frequency and severity, the model has a relatively low degree of uncertainty associated with these factors. In contrast, the model has a high degree of sensitivity to maximum biomass (site productivity), but given the limited observed range for this study area, it also has little influence on uncertainty. The model has a high degree of sensitivity to decomposition rate, and given the possible range in this parameter, it has considerable influence on uncertainty. Finally, the model has a moderate degree of sensitivity to the mortality rate, but modeling indicates the observed variation in mortality rate has little influence on CWD accumulation.

The degree to which each factor influences CWD accumulation also depends on whether the factor's effect is occasional or continuous. The model has low sensitivity to both fire frequency and severity, probably because these influence CWD mass only for the first 100 years after a fire and not for the subsequent 400 or 500 years. The growth rate of the stand is important for the first 80 to 100 years while the stand is growing rapidly and less so afterwards. Site productivity continues to have an influence on CWD accumulation after the stand has reached its peak in mean annual growth. Decomposition, and to some extent mortality rate, have an influence on CWD accumulation every year and, therefore, are important regardless of the age of the stand.

Why Are the Fire Regimes Different?

What factors might be controlling the differences in CWD for the two fire regimes? Modeling results suggest that, all other things being equal, the two fire regimes should have about the same CWD mass. Although the temptation is to attribute differences in CWD mass to fire regime per se, differences in fire frequency and severity can only account for about 10 percent of the observed difference in the amount of CWD predicted by the model. This suggests that, although the mixed-severity regime has about half the CWD of the stand-replacing fire regime, the difference may not be caused by the regime itself. Rather the difference may be due to environment and stand structure. In addition to causing more frequent fires, a warmer, drier environment speeds decomposition, increases fuel consumption, and grows smaller trees (i.e., less biomass).

Model sensitivity analysis indicates that decomposition and fuel consumption may have more effect on CWD mass than fire frequency and severity. Of these two factors, decomposition appears to be the more significant. First, the model is most sensitive to decomposition. Second, estimates of decomposition rates from previous studies vary significantly from 0.018 to 0.029 (Sollins 1982, Spies and others 1988). Third, model simulations using a 0.03 $year^{-1}$ decay rate for the warmer, drier sites having a mixed-severity regime, and a 0.02 $year^{-1}$ for the stand-replacing regime give CWD mass that is 52 percent lower for the mixed-severity regime than the stand-replacing regime. The field data indicate CWD mass is 45 percent lower for the mixed-severity regime. Other research indicates that in this region warm, dry sites have increased decomposition rates, and that excess moisture generally limits log decomposition (Graham 1981, Harmon 1992, Means 1982).

Implications for Management of CWD

CWD mass is much higher in wildfire regenerated stands than in stands intensively managed for timber production (Spies and Cline 1988). To retain functions and processes associated with green trees, some current forestry projects are retaining more live trees in stands in areas that had a mixed-severity regime than in areas with high-severity, stand-replacing regimes. A similar approach could be used for CWD.

To mimic the natural succession of CWD, managers need to consider fire regime, site potential, decomposition rates, fuel consumption, and management objectives. The following questions should be addressed: Does the fire pattern generate the large amounts of CWD of the stand-replacing fire regime or the more frequent, smaller pulses of the mixed-severity fire regime? The latter may be easiest to emulate in stand management, but one should still consider how stand management differs from the CWD cycle of the natural fire regime. Managers should consider whether recent fire history is typical of the natural fire regime or if it bears the influence of post-European settlement burning and suppression. Some information about fire influence may be deduced from the ages of the stands and fire history studies (see examples in Hyderdahl and others 1993). What are the ages of the area's oldest stands in various forest types? What is known about lightning-caused fires and fire suppression? How long since the stand last experienced fire? Managers can also consider the forest structure for its relation to fire severity. Are stands even-aged or do various age cohorts suggest multiple fire-caused stand regeneration events with shade-tolerant as well as shade-intolerant species present? Do stands contain old age cohorts that survived previous fires? If so, what is the proportion of the total stand volume represented by remnant trees?

The rate of decomposition should also be considered, given its substantial effect on total CWD mass through time. On cool and/or wet sites in western Oregon, low temperature and/or high moisture content can limit the activity of decomposing organisms. On the other hand, sites that are excessively dry may also have slow decomposition. The results of this analysis suggest that decomposition rates may vary considerably, even in stands of close proximity, such as those on opposite sides of a ridge.

Finally, managers should consider that the effect of CWD treatments will persist for decades, even centuries. Management strategies may strive to emulate the natural CWD cycle, but may fall short of this goal because of the volume of potential CWD that is removed to the sawmill. For managers to successfully mimic the dead structure associated with the types of fire regimes in this study area, it is advisable to retain the highest levels of CWD in areas having a stand-replacing regime and lesser amounts in areas having a mixed-severity regime.

We suggest a hybrid approach that combines field data and modeling to address difficult management questions. CWD is highly variable through time, and a model of the processes that affect CWD allows us to consider CWD succession, including a much broader range of conditions than can be observed in the field. It also facilitates estimating CWD levels in stages of succession that do not currently exist because of the limited number of fires in the past.

Although the question of "how much" CWD to retain dominates current management discussions, understanding the processes that control CWD and its link with wildlife and fish may be our greatest challenge. In fact, increased understanding of CWD dynamics and functions is our best path not only to answer "how much" but also to understand what is necessary to sustain forest functions. The limited knowledge about the amount of CWD needed to meet ecological objectives points to the need for more discussion between the management and scientific communities on this topic.

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Demographics and Dynamics in Rocky Mountain Forests

Mortality as a Source of Coarse Woody Debris in Managed Stands[1]

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Abstract

Mortality was recorded annually over a 15-year period after thinning in each of three even-aged stands (one ponderosa pine and two ponderosa pine/Douglas-fir/western larch), and after individual tree selection cutting in two uneven-aged ponderosa pine stands. Highest mortality occurred in the controls in both the even- and uneven-aged stands, primarily due to suppression, while weather was the leading mortality agent in the thinning and selection cutting treatments. Beetles were the primary killer of ponderosa pine, and western spruce budworm of Douglas-fir. Mortality of trees ≥25 cm diameter was negligible in all silvicultural cutting treatments. Absent low-intensity fires that historically promoted open pine stands and large-tree development, active management will likely be needed to create desired live tree and dead wood stand components in the future.

Introduction

A primary objective of prescribing and implementing silvicultural cutting treatments in forest management is to achieve a desired future condition in the stand while ensuring long-term site productivity. These treatments typically involve directing site resources toward fewer trees—usually trees of desired species, form, and vigor—thus increasing the growth rate of residual trees. A secondary but traditionally welcome effect of treatment is reduced levels of tree mortality. However, recent insights into ecosystem health suggest that stands consisting only of live trees may not provide the range of conditions needed to support the full suite of life-forms required for sustained ecological function (Cazares and Trappe 1999). Dead trees, either standing or down, are important as food sources (Haverty and Shea 1999, Ross 1999), as refugia for a variety of animal species (Herder and Jackson 2002, Laudenslayer 2002), as substrate for mycorrhizal infection (Harvey and others 1981, Harvey and others 1987), and as a primary source of nutrients and large organic matter for soil development and maintenance (Prescott and Laiho 2002). Therefore, the causes, timing, and distribution of tree mortality, along with silvicultural prescriptions that maintain and/or create relatively large trees on-site, need to be addressed.

This paper reports amounts and causes of tree mortality by diameter, species, and treatment for the first 15 years after various silvicultural cuttings in even- and uneven-aged stands in west-central Montana. Tree mortality has traditionally been

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sampled on relatively small (0.04- or 0.08-ha) plots—plots designed to sample growth of trees, not mortality pattern as part of a larger population. Because tree mortality is often clustered (Dale 1999, Lutes 2002) and episodic, sampling small fixed plots at 5- or 10-year intervals may not be appropriate for discerning mortality relationships and trends. Hence, a combination of small plots (to reflect stand density and structure of live trees) and a complete census of dead trees on much larger plots (to capture the full range of species, distribution, and diameters) was incorporated into this mortality study.

Methods

Tree mortality was monitored in five stands on The University of Montana's Lubrecht Experimental Forest in west-central Montana: a pure, even-aged ponderosa pine *(Pinus ponderosa)* stand; two even-aged ponderosa pine/Douglas-fir *(Pseudotsuga menziesii)*/western larch *(Larix occidentalis)* stands; and two uneven-aged ponderosa pine stands. A thinning demonstration was implemented in 1983 in each of the three even-aged stands to evaluate growth and mortality among three residual densities (6x6, 4x4, and 3x3-m nominal tree spacing) and an unthinned control. A second study was installed in the two uneven-aged ponderosa pine stands in 1984. In this study, growth and mortality were compared among two management treatments—selection cutting with and without underburning—and an untreated control. In the even-aged stands, the thinned units and the control were each about 1.5 ha in size, for a total area of about 6 ha per stand. In the two uneven-aged stands, the selection cutting units and the control were each 1 ha in size, for a total area of 3 ha per stand. This paper reports the amounts and causes of mortality by treatment, species, and diameter for the first 15 years after treatment in each stand.

All five stands are within about 10 km of each other and at nearly the same elevation—1,200 m. At the time the study was initiated, the even-aged ponderosa pine stand was about 80 years old, with 2,620 trees per hectare (tpha), and a basal area density of 45.9 m^2/ha in the control. This stand occupies a site classified as a Douglas-fir/snowberry *(Pseudotsuga menziesii/Symphoricarpus albus)* habitat type (h.t.) (Pfister and others 1977). The two mixed ponderosa pine/Douglas-fir/western larch stands were also about 80 years old at the beginning of the study, with an average of 1,300 tpha, and an average basal area density of 36.7 m^2/ha in the controls. These stands occur on sites classified as Douglas-fir/snowberry h.t. (Pfister and others 1977). Trees in the two uneven-aged ponderosa pine stands ranged in size from seedlings to old-growth trees >75 cm dbh, and from 1 to about 400 years old. One of the uneven-aged stands occurs on a site classified as a Douglas-fir/snowberry h.t., while the other is classified within the Douglas-fir/dwarf huckleberry *(Pseudotsuga menziesii/Vaccinium caespitosum)* h.t. (Pfister and others 1977). At the beginning of the study, the uneven-aged controls supported an average of 950 tpha with an average basal area density of about 23.0 m^2/ha, while basal area density was reduced to 13.8 m^2/ha in the treated stands.

In each stand, all standing dead trees were marked with spray paint at the beginning of the study so that they would not be counted as subsequent mortality. Each autumn, a complete survey (census) of all trees in each stand was conducted to identify trees that had died during the preceding year. Each dead tree was recorded as to species, dbh, and cause of death, and then marked to prevent counting again in subsequent years.

Mortality patterns were similar between the two mixed ponderosa pine/Douglas-fir/western larch stands and between the two uneven-aged ponderosa pine stands; hence results were combined in each case for simplicity of presentation and interpretation. Mortality data from the even-aged stands were combined into 5.0-cm dbh classes for greater resolution in the relatively small range of tree diameters (2.5-45.7 cm), while uneven-aged mortality data were grouped by 10.0-cm dbh classes because of the larger diameter range (2.5-76.2 cm).

Results

Even-aged Ponderosa Pine Stand

Mortality in the pure, even-aged ponderosa pine stand occurred primarily in the uncut control *(fig. 1).* There were 2,620 live tpha in the control at the beginning of the study; however, only 1,774 tpha remained alive at the 15-year remeasurement. Among the three thinning treatments, mortality was greatest in the treatment with 3x3-m nominal spacing, where 35 tpha died in the 15-year period. The 4x4 treatment lost only 15 tpha, and the 6x6 treatment had no mortality. The smallest diameter classes represented in each of the treatments contained the majority of the mortality, while little or no mortality occurred among the largest size classes present in each of the treatments. In the control, 699 tpha died among trees <15.2 cm. The 3x3 treatment lost 27 tpha among trees 7.6-17.8 cm dbh, while the 4x4 treatment lost 15 tpha 12.7-22.9 cm in diameter.

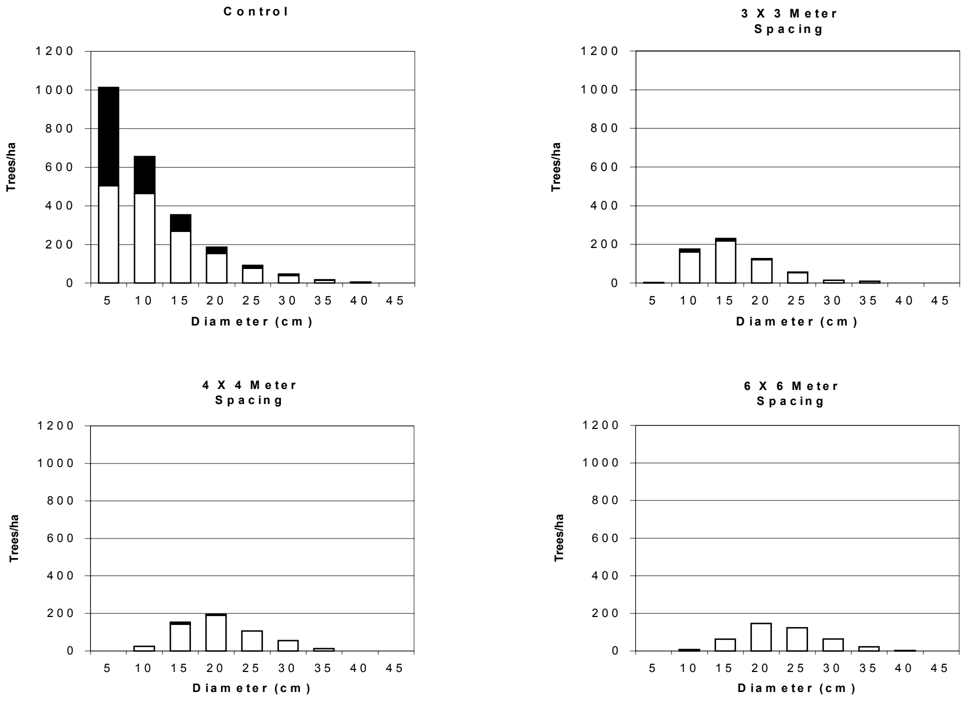

Figure 1—Live trees per hectare by diameter class at the beginning and end of the period 1983–1998 in an even-aged ponderosa pine stand with three thinning treatments and a control. Total bar height indicates live trees in 1983, the shaded portion of each bar indicates trees that died during the 15-year period, and the unshaded portion indicates live trees in 1998.

Causes of mortality in the even-aged ponderosa pine stand varied greatly by tree diameter and treatment *(fig. 2)*. In general, suppression was the primary cause of death in trees <10.2 cm, while bark beetles were the leading cause of mortality among trees >12.7 cm in diameter. Mountain pine beetle *(Dendroctonus ponderosa)* was the primary mortality agent in the 3x3 and 4x4 treatments, accounting for 27 dead tpha in the 10 to 25-cm diameter classes in the 3x3 treatment, and 12 tpha in the 15 and 20-cm diameter classes in the 4x4 treatment. Beetles also killed a total of 252 tpha in the control, primarily among trees 5.1-22.9 cm. Pockets of tree mortality due to mountain pine beetle are common in second-growth ponderosa pine stands, particularly in high-density areas within these stands (Olsen and others 1996). Over the 15-year period, the leading cause of mortality in the control was suppression, killing a total of 682 tpha <12.7 cm. Weather and other agents were minor contributors to mortality across a range of diameters in the control and 3x3 treatment.

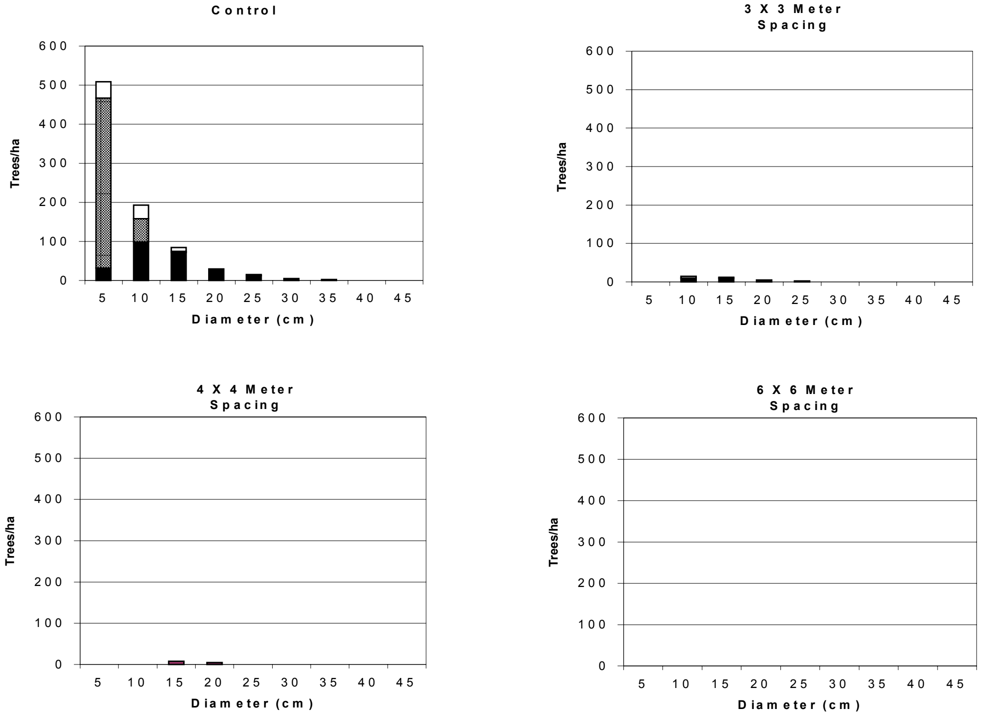

Figure 2—Mortality by diameter class and cause for the period 1983–1998 in an even-aged ponderosa pine stand with three thinning treatments and a control. Dark shading indicates trees killed by bark beetles, stippling indicates trees killed by suppression, and the unshaded portion of each bar indicates trees killed by other causes (primarily weather).

Even-aged Ponderosa Pine/Douglas-Fir/Western Larch Stands

Mortality in the even-aged ponderosa pine/Douglas-fir/western larch stands also occurred primarily in the uncut control *(fig. 3).* There was an average of 1,298 live tpha in the controls at the beginning of the study, which dropped to 954 live tpha at the end of the 15-year period. Among the three thinning treatments, mortality was greatest in the 4x4, with 20 tpha dying in the 15-year period, reducing mean stand density from 467 tpha to 447 tpha. The 3x3 treatments lost an average of 12 tpha, and the 6x6 treatments lost only 5 tpha. Among the treatments in the even-aged mixed conifer stands, the intermediate diameter classes accounted for the majority of the mortality. The 3x3 treatment lost 2 tpha in each 5-cm class from 5.0 to 30.5 cm, while the 4x4 treatment lost 20 tpha in the 10 to 35-cm classes. In the control, mortality was most prevalent among the smaller diameter classes, with an average of 133 tpha and 121 tpha dying in the 5- and 10-cm dbh classes, respectively.

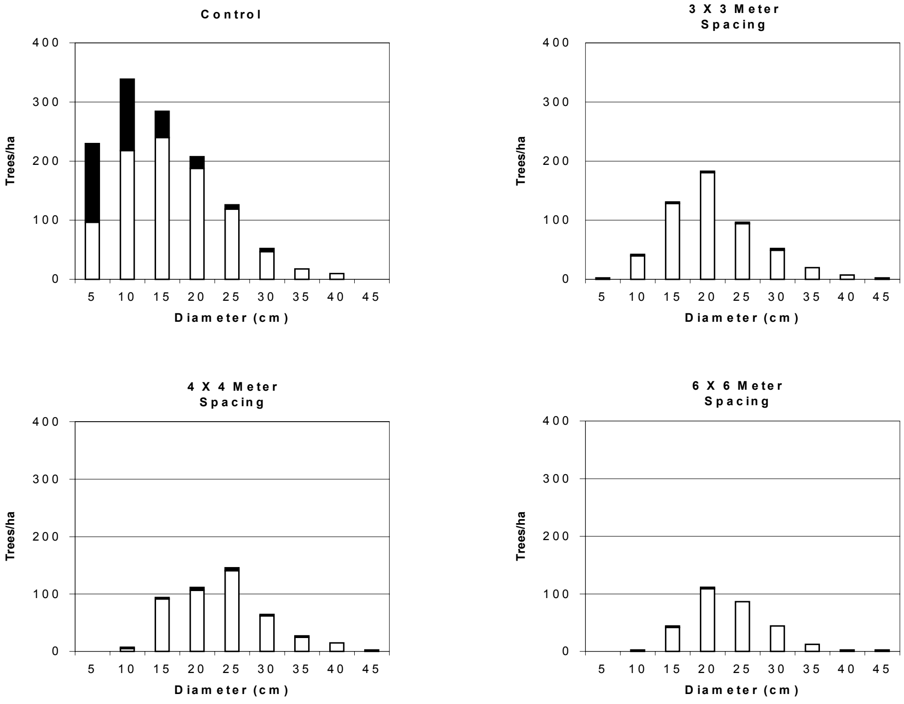

Figure 3—Live trees per hectare by diameter class at the beginning and end of the period 1983–1998 averaged for two even-aged mixed-conifer stands with three thinning treatments and a control. Total bar height indicates live trees in 1983, the shaded portion of each bar indicates trees that died during the 15-year period, and the unshaded portion indicates live trees in 1998.

Causes of mortality in the even-aged ponderosa pine/Douglas-fir/western larch stands varied by tree species, diameter, and treatment *(fig. 4).* Suppression and western spruce budworm *(Choristoneura occidentalis)* were the primary causes of death of Douglas-fir in the controls, whereas mountain pine beetle was the primary killer of ponderosa pine. Virtually no western larch died in either of the mixed-species stands. In general, suppression was the leading cause of mortality in the controls, while weather and beetles were primarily responsible for mortality in the 3x3 and 4x4 nominal spacing treatments. In the controls, suppression killed an average of 156 tpha <20.3 cm, while beetles and weather led to the death of 124 tpha 5.1-35.6 cm in diameter. Western spruce budworm also accounted for the death of 62 tpha <25.4 cm in the control, where the host species (Douglas-fir) was more abundant, the trees were over-stocked and stressed, and a multistoried canopy provided better larval habitat (Carlson and Wulf 1989). Neither suppression nor budworm was an agent of mortality in the thinning treatments, where beetles and weather were responsible for the mortality of 5 tpha in the 3x3 treatment and 12 tpha in the 4x4 treatment.

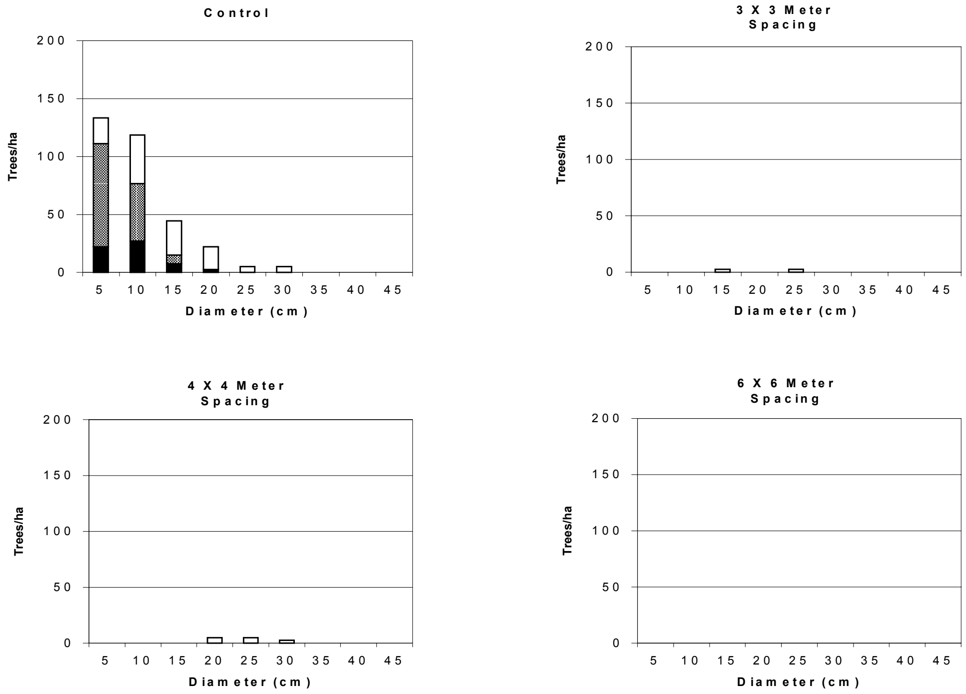

Figure 4—Mortality by diameter class and cause for the period 1983–1998 averaged for two even-aged mixed-conifer stands with three thinning treatments and a control. Dark shading indicates trees killed by budworm, stippling indicates trees killed by suppression, and the unshaded portion of each bar indicates trees killed by other causes (primarily weather and bark beetles).

Uneven-aged Ponderosa Pine Stands

Mortality in the uneven-aged ponderosa pine stands was greatest in the uncut controls *(fig. 5)*. There was an average of 951 live tpha in the controls at the beginning of the study, and 759 live tpha at the end of the 15-year period. In the two selection cutting treatments, mortality was greatest in the cut/burn treatment, with an average of 59 tpha dying in the 15-year period, reducing mean stand density from 326 tpha to 267 tpha. The cut/no-burn treatment lost 30 tpha, reducing stand density from 353 tpha to 323 tpha. The smallest diameter classes contained the majority of the mortality in the two selection cutting treatments. The cut/burn treatment lost an average of 54 tpha <25.4 cm, while the cut/no-burn treatment lost only 25 tpha <25.4 cm. In the control, mortality was also highest among the smaller diameter classes, with an average of 156 tpha <25.4 cm dying in the 15-year period. Fewer than 2 tpha ≥35.6 cm died in either of the selection treatments, while more than 5 tpha died among similarly sized trees in the control.

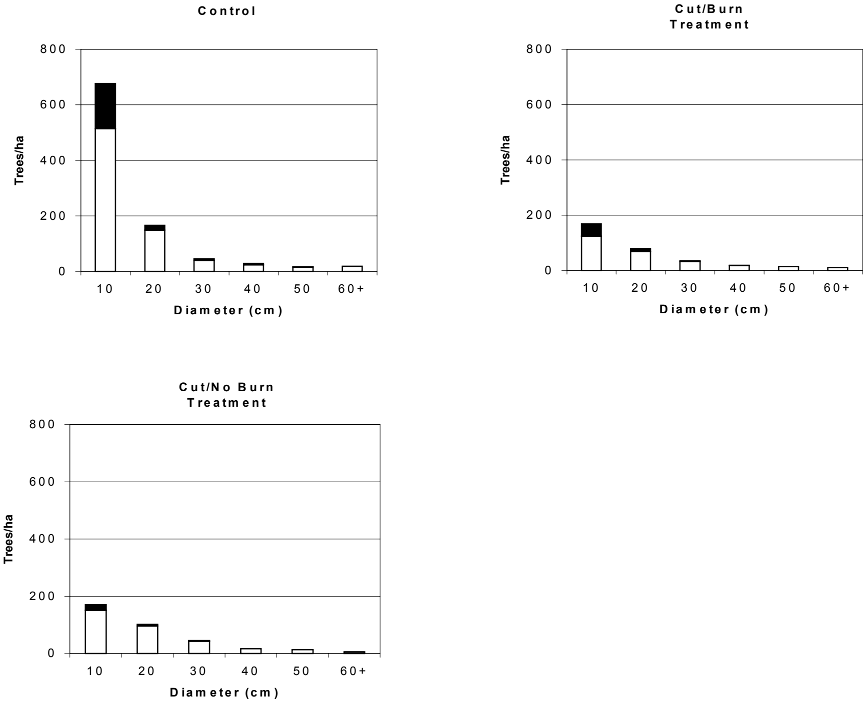

Figure 5—Live trees per hectare by diameter class at the beginning and end of the period 1984–1999 averaged for two uneven-aged ponderosa pine stands with two selection cutting treatments (with and without burning) and a control. Total bar height indicates live trees in 1984, the shaded portion of each bar indicates trees that died during the 15-year period, and the unshaded portion indicates live trees in 1999.

Causes of mortality in the uneven-aged ponderosa pine stands varied primarily by treatment *(fig. 6)*. In general, suppression was the dominant cause of mortality in the controls, fire was the leading cause of mortality in the cut/burn treatments, and weather was the primary agent in the cut/no-burn treatments. Mortality due to bark beetles was present in both treated and untreated portions of the stands, though it was much higher in the untreated portions, where higher densities created conditions more favorable for beetles. In the controls, suppression killed an average of 99 tpha <15.2 cm, while beetles caused the death of 52 tpha <45.7 cm. Weather accounted for an average of 44 dead tpha <25.4 cm in the control, 15 dead tpha <25.4 cm in the cut/burn treatment, and 20 dead tpha <35.6 cm in the cut/no-burn treatment. Fire killed an average of 32 tpha <15.2 cm and 5 tpha between 15.2 and 25.4 cm in the cut/burn treatment. Beetles accounted for the death of 7 tpha <35.6 cm in the cut/burn treatment and 5 tpha <25.4 cm in the cut/no-burn treatment. Other agents, including root rot, budworm, and animals, killed an average of 3 tpha <15.2 cm among the cut/no-burn treatments.

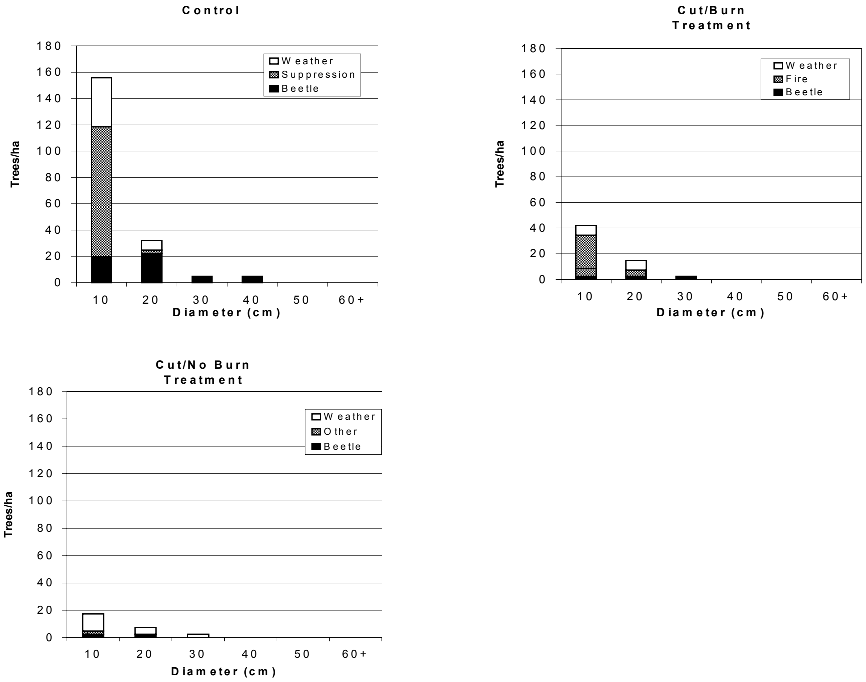

Figure 6—Mortality by diameter class and cause for the period 1984–1999 averaged for two uneven-aged ponderosa pine stands with two selection cutting treatments (with and without burning) and a control. Dark shading indicates trees killed by bark beetles; stippling indicates trees killed by suppression, fire, or other causes (according to treatment); and the unshaded portion of each bar indicates trees killed by weather.

Discussion

Mortality for the 15-year period was greatest in the untreated controls for both the even- and uneven-aged stands. Mortality in the even-aged stands was lowest in the low-density (6x6 nominal spacing) thinning treatment. In the uneven-aged stands, mortality was lowest in the cut/no-burn treatment. Suppression was the leading cause of mortality among the uncut controls in all stands, primarily affecting trees in the smallest diameter classes, while beetles were the leading cause of mortality among the larger size classes in the ponderosa pine stands.

These findings indicate that the thinnings and selection cuttings tended to reduce total mortality. However, this reduction in mortality was not distributed evenly across the diameter classes. Mortality levels among small-diameter trees in the treatments were consistently much lower than mortality levels of small-diameter trees in the controls. However, mortality differences among treatments and controls were not as significant for the large-tree stand component. Although overall mortality of large trees was reduced by treatment, mortality of large trees was not entirely prevented by treatment. The susceptibility of larger pines to bark beetle attack was likely reduced by the increased tree vigor resulting from thinning or selection cutting. However, scorch from prescribed burning likely stressed some residual trees in the selection cut/burn treatment, and may have increased susceptibility to beetle attack. Untreated forest with favorable habitat for pests near treated areas may have allowed insects access to those larger trees stressed by prescribed burning.

One important observation over the 15-year monitoring period was the relatively low mortality of small trees after prescribed underburning in the individual tree selection study. Prescribed burning has been questioned as an appropriate treatment in uneven-aged stands because of the potential to incinerate trees in the smaller diameter classes. However, over the 15-year period, fewer than 20 percent of the trees in the 10-cm class died as a result of burning, and only about 25 percent died from any cause. These results indicate that judicious use of prescribed burning can achieve a variety of management objectives, such as preparing seedbeds, killing small firs, reducing activity fuels, and stimulating growth of important wildlife forage species (e.g., willow *(Salix* spp.) and bitterbrush *(Purshia tridentata)* [Ayers and others 1999]), while limiting mortality of small pines to acceptable levels.

Conclusions

The two types of silvicultural cuttings evaluated in this study—thinning and selection cutting—were found to reduce mortality in even-aged and uneven-aged ponderosa pine stands, respectively. This would be considered a positive outcome from a timber production point of view. However, it may be less desirable when viewed in the broader context of maintaining conditions favorable to indigenous fauna and flora in managed ponderosa pine and drier mixed conifer ecosystems. Because mortality was highest in the smallest diameter classes in all stands, relatively large snags and downed logs may need to be manufactured in managed stands when desired for wildlife or other ecological considerations.

Standing dead wood may be created by girdling live trees with an axe or chainsaw, baiting with pheromones, inoculating with decay fungi, or burning to kill either the cambium at the base of the tree, the roots, or the foliage and terminal bud. However, as several investigators (Boleyn and others 2002, Parks 1999, Shea and others 2002) reported at this symposium, not all dead trees are created equal. For example, woodpecker foraging occurred primarily in the younger age classes of snags (Farris and others 2002). Huss and others (2002) found that woodpecker nest trees were frequently infected by the red-belted conk fungus *(Fomitopsis pinicola),* and Laudenslayer (2002) noted that snags with historical and active nests of cavity-nesting birds tended to be taller and had greater diameters than those without nests. In addition to the size of snag and time since death, how a tree dies may have profound effects on how long it remains standing and what function(s) it may serve (Bull 1983, Bull and Partridge 1986, Keen 1955). Thus, habitat suitability of dead trees and logs for various wildlife species should be considered when selecting which trees are to be killed and how to kill them (Bull and others 1980).

Maintaining desired amounts of large snags and logs both in the near and distant future may require silvicultural stand interventions that not only kill and remove trees from the stand but also leave some dead trees (Ffolliott 1983). The large live and dead trees present in today's ponderosa pine stands developed under stand densities widely documented to be more open than current conditions (Arno and others 1995, Covington and Moore 1994). The low-intensity fires that historically accomplished thinning are often not possible under current stand conditions, given heavy down-fuel loading and the presence of sapling and pole ladder fuels (Fiedler and others 1998). Historically, periodic low-intensity fires commonly created open stand structures, lowered fuel loadings, and favored survival and development of large-diameter, fire-resistant pines. Absent this natural process to reduce density and discriminate against Douglas-fir/true firs, development of large pines in the future will likely require well-designed silvicultural cuttings to release trees, reduce ladder fuels, and simultaneously create desired standing and down coarse woody debris structures. Such cuttings have been shown to significantly increase diameter growth across the full range of tree diameters (including old-growth trees) in uneven-aged ponderosa pine stands (Fiedler 2000). It seems unlikely that productive, ecologically functional, and sustainable ponderosa pine ecosystems will attain these desired conditions without actively managing both live-tree and dead wood stand components.

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Snags and Down Wood in the Interior Columbia Basin Ecosystem Management Project[1]

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Abstract

Snags and down wood are major ecosystem and wildlife habitat components of the Interior Columbia Basin ecosystem. Their natural abundance and distribution have been altered by decades of land conversion, fire suppression, and timber and firewood harvest, but the degree and pattern of change have been open to question. Consequently, an analysis of the changes that have occurred was a required element of the Interior Columbia Basin Environmental Impact Statement. Members of the Science Advisory Group of the Interior Columbia Basin Ecosystem Management Project modeled snag and down wood abundance at the landscape level for the project analysis area. We constructed 10 density tables for combinations of 3 Potential Vegetation Groups, 2 temporal regimes, 2 fire regimes, and 2 public land management characterization classes. Snags and down wood were divided into two size classes, small and large, with a 53 cm DBH break point, and a 13 cm minimum DBH. Forest stands were placed into one of four categories: early-seral, mid-seral, late-seral single-strata, and late-seral multistrata. We defined five categories of snag and down wood abundance: none, rare, uncommon, common, and abundant. Each size class/abundance category combination, such as large snag/common, small down wood/rare, etc. had its own unique density range. We combined computer simulations using the Columbia River Basin Succession Model with geographic information system (GIS) data layers to project historical (pre-settlement) and current snag and down wood densities. We also made long-term (100 year) projections of snag and down wood trends based on the three public land management alternatives described in the Interior Columbia Basin Supplemental Draft Environmental Impact Statement. Our models for the Basin as a whole showed small and large snag abundances currently below the historical levels, and small and large down wood amounts currently greater than historical levels. The 100 year simulations projected small snag amounts returning to historical levels, large snag amounts increasing above current levels but not returning to historical amounts, and the small and large down wood amounts generally decreasing from current levels but remaining above historical levels.

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Introduction

The Interior Columbia Basin Ecosystem Management Project, (ICBEMP), was established by charter in 1994. The charter, signed by the Chief of the USDA Forest Service (FS) and the Director of the Bureau of Land Management (BLM), provided instruction to the agencies to develop specific products that would lead to the adoption of a scientifically sound, ecosystem-based strategy for managing FS- and BLM-administered lands within the Interior Columbia Basin (ICB or "the Basin"). The charter also required the preparation of a Basin-wide Environmental Impact Statement (EIS). Quigley and Arbelbide (1997) developed an assessment of ecosystem components that described the ecological, social and economic conditions in the Basin. Two separate but complementary draft environmental impact statements (DEIS), known as the Eastside DEIS and the Upper Columbia River Basin DEIS (USDA Forest Service and USDI Bureau of Land Management 1997a, USDA Forest Service and USDI Bureau of Land Management 1997b), were prepared. Quigley and others (1997) developed a scientific evaluation of the management alternatives described in the DEIS documents. Subsequently, a supplemental draft environmental impact statement (SDEIS, USDA Forest Service and USDI Bureau of Land Management 2000) was issued to address public comments concerning the DEIS. Our work built from the landscape ecology portion (Hann and others 1997) of the assessment of ecosystem components (Quigley and Arbelbide 1997) and was part of an evaluation of long-term effects of the three management alternatives described in the SDEIS (USDA Forest Service and USDI Bureau of Land Management 2000).

The SDEIS contains three alternatives for the management of FS- and BLM-administered lands in the Basin. We will not describe them in detail here, but present a very brief summary of the key focus of each alternative (more detail is available at the Web site: http://www.icbemp.gov).

Alternative S1 is termed the "no action" alternative. The term "no action" does not mean that no management will take place. It means that management of FS- and BLM-administered public lands would continue based on the land use plans that are currently in place, including existing policies, U.S. Fish and Wildlife Service and National Marine Fisheries Service Biological Opinions, and Healthy Rangelands standards and guidelines. Analysis of a "no action" alternative is a requirement of the National Environmental Policy Act of 1976 (NEPA) and BLM and FS planning procedures.

Alternatives S2 and S3 are termed "action" alternatives that are meant to improve the clarity, focus, and ability to implement the proposed management direction. In general, the two action alternatives were designed to:

- Integrate landscape, disturbance regime, aquatic, terrestrial, socio-economic, and tribal components into one ecosystem management strategy;
- Protect important aquatic and terrestrial habitats;
- Identify priority areas for restoration; and
- Provide a link to existing management direction through a step-down process that will combine some land designations with management flexibility at the local level.

A key emphasis of alternative S2 is to minimize short-term risks, especially to threatened, endangered, or proposed species, important species habitats, and riparian areas. The intent of the alternative is to put a greater emphasis on conducting detailed analysis prior to conducting management activities. Areas are prioritized for restoration in order to make management activities more effective and efficient.

Alternative S3, on the other hand, has a stronger emphasis on more quickly addressing long-term risks from either management activities or natural disturbance events; there is less of an emphasis on analysis. There is also a stronger focus on locating management activities where they can benefit isolated and/or economically specialized communities.

Snags and down wood are essential ecological components of the ICB ecosystem. Standing snags provide foraging, roosting, denning and nesting habitat for a number of wildlife species (Bull and others 1997, Marcot and others 1997, Thomas 1979, Wisdom and others 1999). As snags decay and fall to the ground, and become down wood, they provide food and shelter for different species (Bartels and others 1985, Maser and others 1979). Down wood also stores nutrients and moisture, and aids in soil development. Down wood in stream channels influences channel morphology; especially in forming pools and in-stream cover, retention of nutrients, and storage and buffering of sediment (Lee and others 1997).

Analysis of changes in snag and down wood densities across the Basin from historical times to the present may provide valuable insight into their management for the future. In this paper we describe the manner in which the snag and down wood abundance values were determined in the ICBEMP, their modeled current conditions in the Basin, and projected density trends after 100 years under three public land management alternatives.

Study Area

The ICBEMP analysis area *(fig. 1)* covers approximately 58 million hectares (145 million acres) in the states of Washington, Oregon, Idaho, Montana, Wyoming, Nevada and Utah—an area approximately the same size as the country of France.

Public lands managed by the Forest Service and Bureau of Land Management account for 53 percent of the Basin. This represents approximately 25 percent of all FS-administered lands and 10 percent of all BLM-administered lands in the lower 48 states. Approximately 4 million hectares (10 million acres) in the Basin are federally designated wilderness, accounting for nearly one-third of all federally designated wilderness lands in the contiguous states. The study area also includes about 20 percent of the area in the lower 48 states that is American Indian reservation. The amount of timber harvested in the Basin accounts for approximately 10 percent of the total for the entire United States (Quigley and others 1996). Elevations in the Basin range from less than 150 meters to more than 3,000 meters above mean sea level. The average annual precipitation values are highly variable, and range from less than 20 to more than 250 centimeters per year (USDA Forest Service and USDI Bureau of Land Management 1997). More than 17,000 plant and animal taxa occur in the study area, including 609 known vertebrate taxa (Arbelbide and Quigley 1997). At present, the Basin contains 29 threatened or endangered species, including 16 fish species or species stocks.

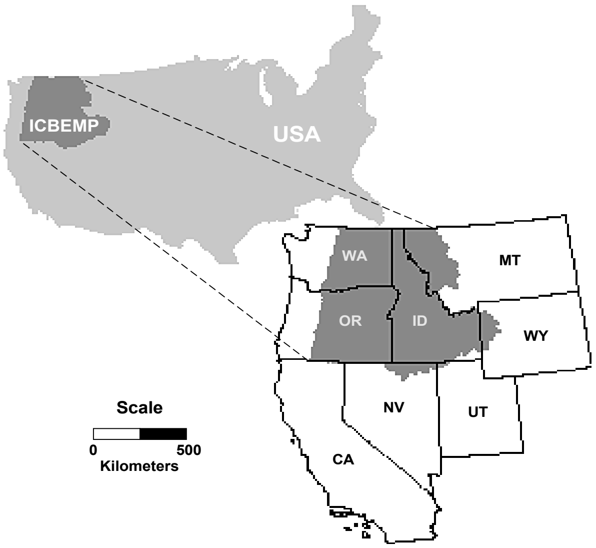

Figure 1—The Interior Columbia Basin Ecosystem Management Project (ICBEMP) analysis area.

Methods

Snag and Down Wood Tables

Members of the Science Advisory Group (SAG) formulated the snag and down wood density tables through an iterative process of literature review and discussions with experts. Our original tables, based on proposals put forward by the Environmental Impact Statement team, consisted of four forest stand classes (early-seral stands, mid-seral stands, late-seral single-strata stands, and late-seral multi-strata stands) and six Potential Vegetation Group (PVG)/land management combinations (e.g. Cold, Moist or Dry Forest, managed or unmanaged stands). Four tables, for current large and small snags and down wood, were constructed. We populated the 24 cells of each table with snag and down wood per-hectare values derived from the literature.

It quickly became apparent to us that the amount of usable data available from the literature was inadequate to populate most of the cells with values. We found that many published reports divided snags and/or down wood into size classes that could not be adapted to ours. Furthermore, many studies reported snag and down wood densities by vegetation types or age classes that we could not match. Differing units of measure were also a problem. For example, down wood amounts reported in square meters or tons per hectare could not be accurately converted to pieces per hectare. Attempts to fill the holes in the tables with values from the Forest Inventory Analysis (FIA) and Current Vegetation Survey (CVS) databases were ruled out due to the lack of comprehensive coverage.

Following discussions with snag and down wood experts and members of the EIS team we revised the format of the snag and down wood tables. The new format contained the same four forest succession/structure stages as before, but we now included a live tree component as a comparison to our snag and down wood amounts.

Live trees, snags, and down wood were all divided into small and large sizes. The small/large breakpoint was 53 centimeters (21 inches) diameter at breast height (DBH). "Small" did not include trees, snags, or down wood less than 13 centimeters (5 inches) DBH. These values were taken from the tree DBH size classes defined by Oliver (1981), modified by O'Hara and others (1996), and used throughout the CRBSUM modeling process (Keane and others l996). The values were also commonly used in the literature on cavity nesting animals, particularly birds (Raphael and White 1984, Saab and Dudley 1998).

The new tables also used tree, snag, and down wood density categories instead of individual density values. The categories were none, rare, uncommon, common, and abundant. Each category represented a range of per-hectare values, and each forest component such as large snag, small down wood, etc. had its own definition for each category (e.g. "rare" for small live trees did not have the same value range as "rare" for large down wood). We also added two fire regimes (high-frequency low-intensity fires and low-frequency high-intensity fires) to the tables. There were 10 tables in all, covering 3 PVGs (Cold, Moist, and Dry Forest) 2 temporal regimes (historical and current), 2 fire regimes, and 2 management categories (unmanaged and managed):

1. Cold forest, historical conditions, low-frequency high-intensity fire regime;
2. Cold forest, historical conditions, high-frequency low-intensity fire regime;
3. Moist forest, current conditions, low-frequency high-intensity fire regime, unmanaged;
4. Moist forest, current conditions, low-frequency high-intensity fire regime, managed;
5. Moist forest, historical conditions, low-frequency high-intensity fire regime;
6. Moist forest, historical conditions, high-frequency low-intensity fire regime;
7. Dry forest, current conditions, low-frequency high-intensity fire regime, unmanaged;
8. Dry forest, current conditions, low-frequency high-intensity fire regime, managed;
9. Dry forest, historical conditions, low-frequency high-intensity fire regime;
10. Dry forest, historical conditions, high-frequency low-intensity fire regime.

We did not include managed conditions for cold forests because, for the most part, cold forests have not received extensive management and their fire regimes are relatively unaltered from historical conditions. The term "historical" refers to the conditions that existed prior to Euro-American settlement of the Basin. Historical and current live tree, snag, and down wood values were based on applicable literature values, expert opinion, and CRBSUM modeling. We submitted the revised tables to experts for review and held meetings to discuss the table attributes, our assumptions concerning density categories, snag and down wood dynamics, etc. before a final set of 10 tables was considered acceptable.

Geographic Information Systems

Geographic Information System (GIS) modeling of the snag and down wood abundances across the Basin required a sequence of computations and data layer combinations that can be generalized into four major processes. First, the GIS team created a continuous Basin-wide vegetation layer at a one-kilometer scale. This layer was a combination of terrestrial community groups with dominant physiognomic types and potential vegetation groups for the historical, current, and simulated future conditions of the Basin (see Hann and others [1997] and Keane and others [1996] for a detailed discussion on the treatment of vegetation in the ICBEMP). This layer provided the necessary baseline information on forest vegetation, including successional stage and stand structure. A subsequent combination of this layer with a layer describing ecological disturbances was then produced to add information on fire regimes.

In the second step, the GIS team combined the vegetation layers with a layer detailing the various management prescriptions defined for each of the proposed alternatives in the SDEIS. The resulting layer was the basis for different snag and down wood management scenarios and allowed comparison of snag and down wood levels under the SDEIS alternatives.

The third step linked the data from the snag and down wood tables constructed by the SAG with the vegetation layers described in step one. In this third step, the GIS team assigned both snag and down wood density categories and category midpoints to the vegetation data, and included the different management prescriptions and proposed SDEIS alternatives. The resulting layers provided data about snag and down wood amounts across the Basin for the historical, current, and long-term (100 year) conditions under three proposed management alternatives.

In the fourth step the GIS team calculated a weighted average of density per subwatershed (6th code Hydrologic Unit or HUC6 level) for small and large snags and down wood for the historical, current, and simulated 100-year conditions of the Basin. This step allowed the analysis and summation of snag and down wood amounts according to various political, management, and land ownership units.

Results and Discussion

Our results discussed are preliminary and subject to revision, as is the SDEIS document itself. All figures and maps are also draft documents and are subject to revision. We used snag and down wood amounts based on the vegetation in the historical scenario as the baseline for our comparisons. We present results for only the FS/BLM-administered lands and Interior Columbia Basin as a whole.

Current Conditions

Our models indicated that small snag amounts increased slightly (7 percent) from the historical conditions on FS/BLM-administered lands but declined by 14 percent across the Basin *(fig. 2)*. Most of the increase on FS/BLM lands occurred in the Dry Forest PVG, with some minor increases in the Cold Forest PVG. This occurred because the amount of forests in the mid-seral stage increased in the Dry Forest PVG, while the amount in the late-seral stage declined. In general, mid-seral stage forests contain fewer small snags per hectare than the late-seral forest, especially in managed areas (Ohmann and Waddell, 2001). However, much of the increase in mid-seral forests on FS/BLM lands occurred in unroaded and wilderness areas. In these areas, fire suppression allowed development of dense stands of stressed, shade-tolerant trees having low resistance to insect and disease attack and, consequently, abundant small snags. Declines of small snags in the northern Rocky Mountains of Montana and Idaho and the foothills of the Cascade, Wallowa and Blue Mountains of Oregon *(fig. 3)* were more than offset by increases in much of central Idaho, the northern Cascade Mountains of Washington, portions of the southern Cascade, Wallowa, and Blue Mountains in Oregon, and in the Teton Mountains of Wyoming.

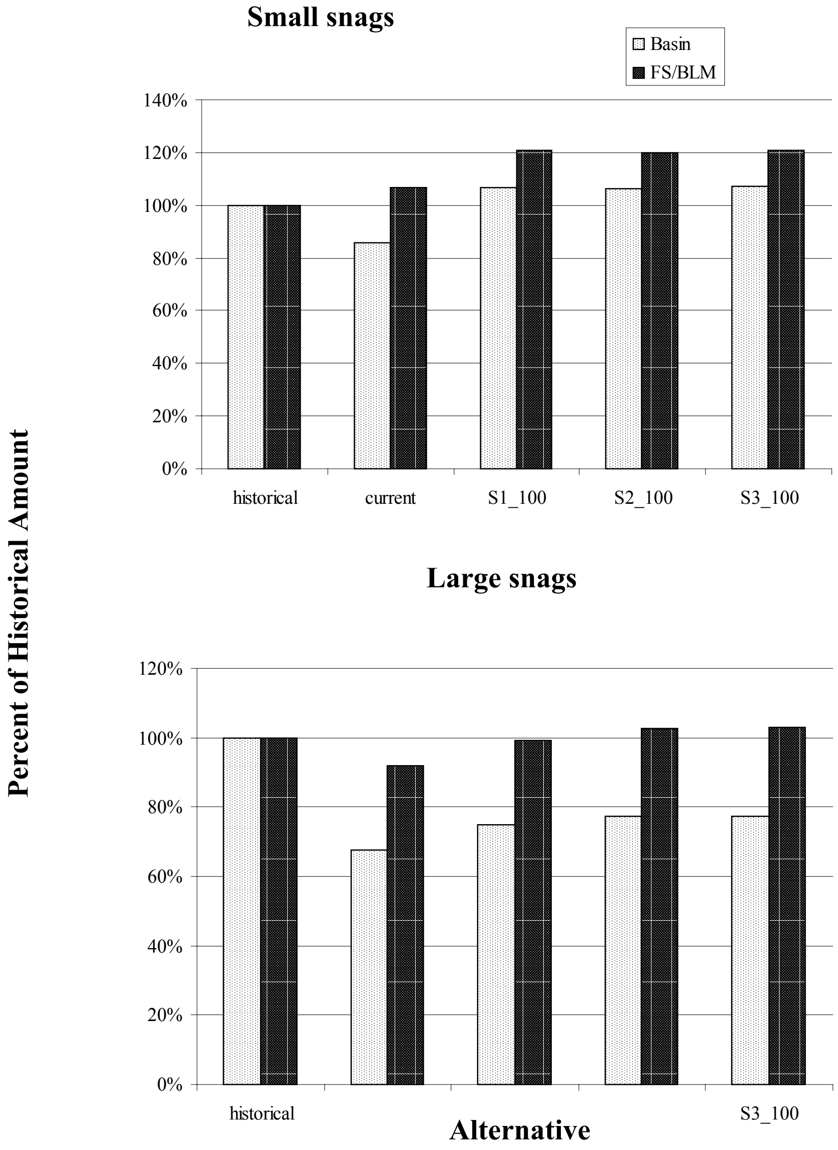

Figure 2—Small snag and large snag amounts as a percentage of the historical amounts for forest PVGs on FS/BLM ICBEMP lands and for the total Interior Columbia Basin. Sl_100, S2_100 and S3_100 represent the values after a 100-year simulation of the SDEIS management alternatives.

Large snag amounts declined by approximately 8 percent on FS/BLM-administered lands and 31 percent across the Basin, compared to the historical levels *(fig. 2).* The largest losses occurred in the Dry Forest and Moist Forest PVGs due to increases in mid-seral forests and decreases in late-seral forests. Late-seral stage forests typically contain higher levels of large snags. Large, fire-created snags may also be present in early-seral forests, but usually fall quickly. Few large snags remain standing into the mid-seral stage (Everett and others [In press]). There are generally fewer surviving large trees in early and mid-seral forests and, hence, reduced sources for new large snag recruitment. Furthermore, the new cohort of live trees does not become large enough to generate large snags until well into the mid-seral stage and often not until the late-seral stage. This may produce a "U-shaped" pattern of abundance described by Franklin and Spies (1991) similar to the "boom and bust" cycle discussed by Everett and others [In press]). Large snag declines on FS/BLM lands are compounded in managed or roaded areas by harvest and firewood cutting. The spatial pattern was very similar to that of the small snags; however, greater declines occurred in the Wallowa and Blue Mountains and the central and southern Cascade Mountains *(fig. 3).*

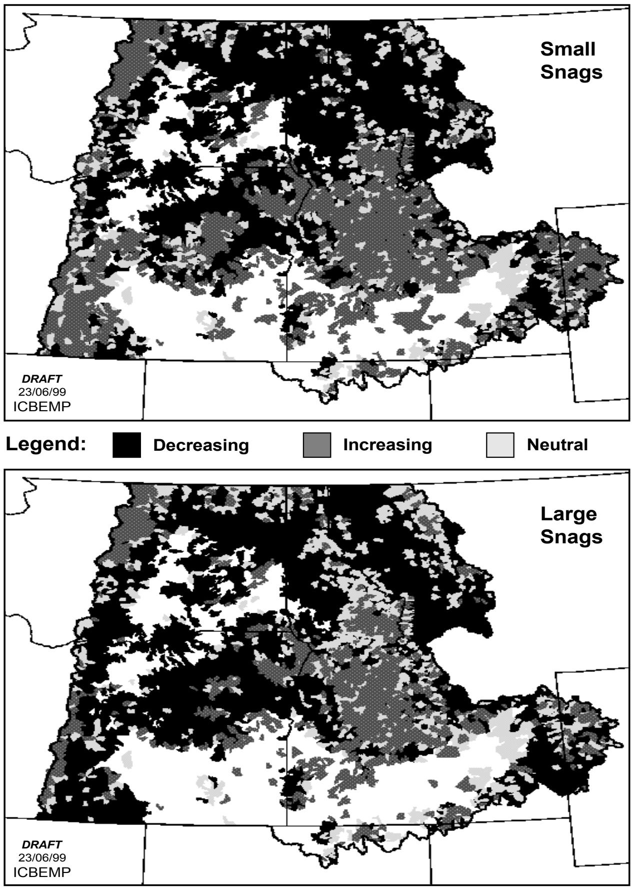

Figure 3—Current distribution of small snags and large snags trends across the Interior Columbia Basin. Neutral represents a value that is with 30 percent, positive or negative, of the historical level. Decreasing represents a decline of more than 30 percent, and increasing represents an increase of more than 30 percent. Unshaded areas represent non-forested lands.

Small and large down wood amounts have increased from the historical levels on both FS/BLM-administered lands and across the Basin *(fig. 4)*. In general, down wood has a longer 'life-span' than snags (Bartels and others 1985, Beukema and others 1999, Cline and others 1980, Lambert and others 1980, Maser and others 1979, Parks and Shaw 1996, Spies and others 1988, Stevens 1997,1999). The large numbers of trees killed by fires in the early- to mid-1900s generally are no longer present as snags, but are often present as down wood. Fire suppression often results in over-dense stands prone to insect and disease outbreaks. These conditions favor the recruitment of smaller down wood since small trees are more numerous than large trees and small snags usually fall sooner than large snags (Beukema and others 1999,

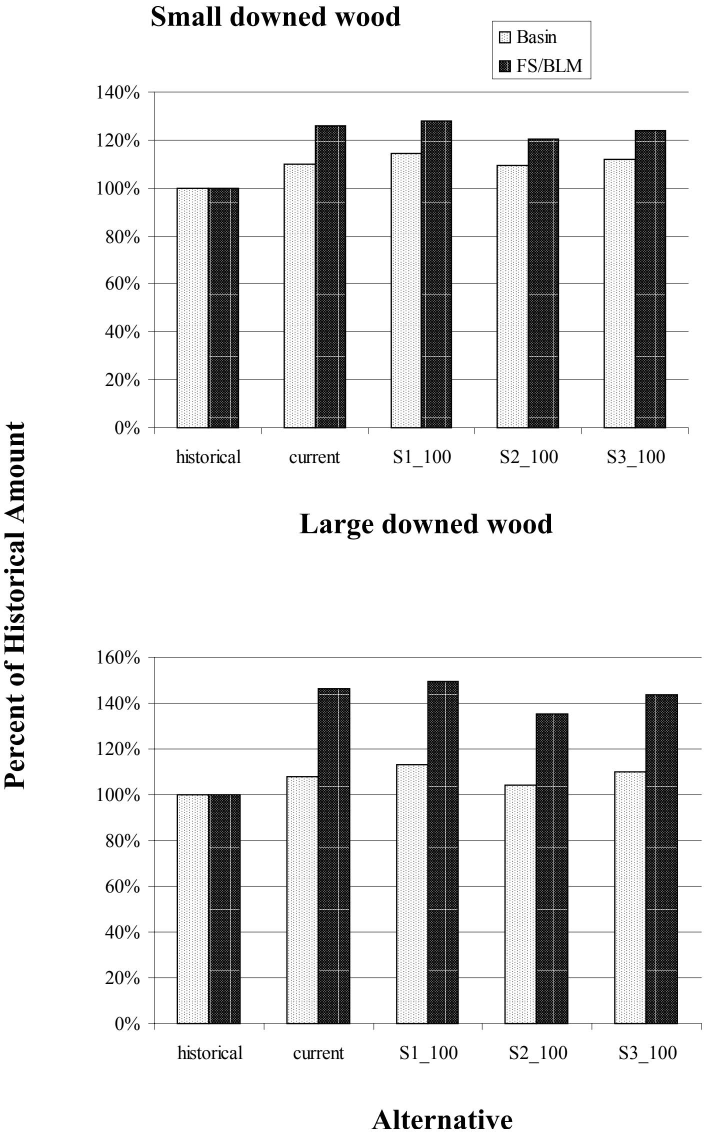

Figure 4—Small down wood and large down wood amounts as a percentage of the historical amounts for forest PVGs on FS/BLM lands and for the entire Interior Columbia Basin. S1_100, S2_100, and S3_100 represent the values after a 100-year simulation of the SDEIS management alternatives.

Bull 1983, Bull and others 1980, Cline and others 1980, Everett and others in press, Huggard 1997, Morrison and Raphael 1993, Neitro and others 1985, Raphael and Morrison 1987, Raphael and White 1984). Large down wood pieces tend to last longer, however, perhaps resulting in similar increases over time.

Small down wood amounts increased from the historical levels by 25 percent on FS/BLM lands and about 10 percent across the Basin *(fig. 4)*. In both cases, the increases occurred mostly in the Dry Forest PVG because of large increases in mid-seral stage forests. Although the mid-seral forests usually do not contain as much small down wood as the late-seral forests, the increase in the area of dense, over-crowded mid-seral forests generated by fire suppression produced abundant small down wood on FS/BLM lands, especially in unroaded and wilderness areas. Most of the increases took place in central Idaho, Washington's north Cascade Mountains, and Oregon's south Cascade, Wallowa, and Blue Mountains *(fig. 5)*. Declines occurred in small areas, especially in east-central Washington (the southern Selkirk Mountains), along the central Oregon/Washington border, and in far northwest Montana (the Salish and Purcell Mountains).

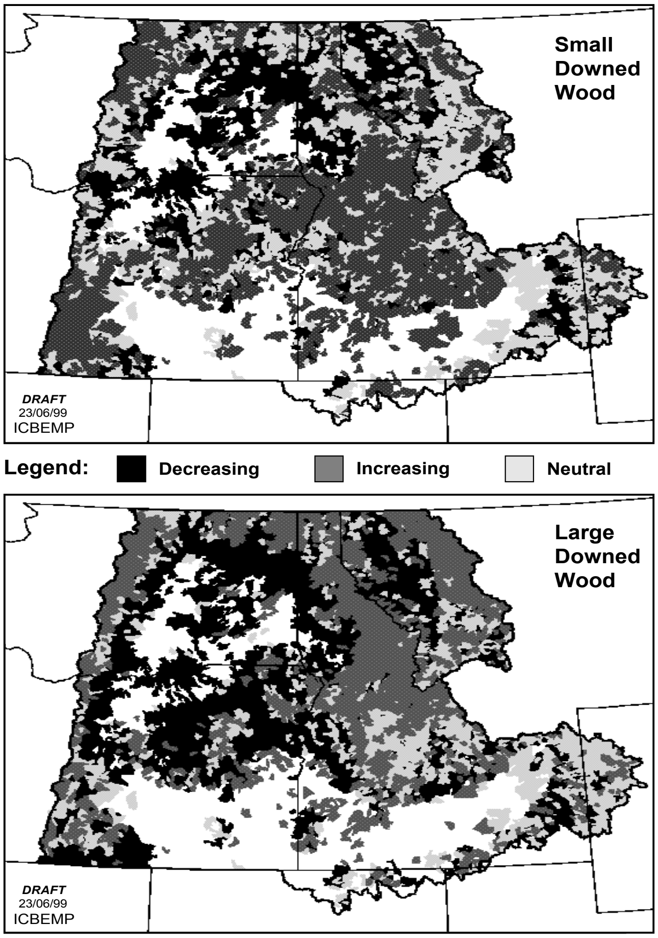

Figure 5—Current distribution of small down wood and large down wood trends across the Interior Columbia Basin. Neutral represents a value that is with 30 percent, positive or negative, of the historical level. Decreasing represents a decline of more than 30 percent, and increasing represents an increase of more than 30 percent. Unshaded areas represent non-forested lands.

Amounts of large down wood increased substantially from historical levels on FS/BLM lands and, to a lesser extent, Basin-wide *(fig. 4)*. In both cases, the greatest increases occurred in the Moist Forest PVG. Large down wood pieces can be very long-lived. Large snags created by fire, insect and disease attack often fall within 10 to 30 years (Bull 1983, Harrington 1996, Keen 1929, Lyon 1977, Mitchell and Preisler 1998, Schmid and others 1985), though some may last much longer (Hillis 1999 personal communication). This means that large down wood amounts are generally greater than large snag amounts in the late-seral stage (Ohmann and Waddell 2000). Increases in large down wood levels on FS/BLM lands are most likely due to a larger proportion of acres in non-roaded and wilderness areas where there is less removal of large down wood and large snags. The increases were found throughout much of central and northern Idaho, northwest Montana, northeast Washington, and the northern and southern Cascade Mountains *(fig. 5)*. Areas that exhibited declines in large down wood amounts included northwest Montana, much of the Washington and Oregon Cascade foothills, the lower elevation forests of northeast Washington, and the mid and lower elevation Blue and Wallowa Mountains in Oregon. Only a few areas of south-central Idaho and northeast Wyoming showed no change.

Long-Term Future Conditions

Both small and large snag levels increased above current levels under all SDEIS management alternatives *(fig. 2)*. Small snag levels increased by about 10 percent above current conditions on FS/BLM lands after 100 years under all three alternatives. The largest increase (for all alternatives) was in the Moist Forest PVG where the amount of late-seral stage forest increased greatly in all simulations. This increase was driven by the successional transition of large amounts of mid-seral to late-seral stage forests over 100 years. Small snags are common in the late-seral forests and amounts will continue to increase as succession progresses. Across the Basin, small snags increased beyond the current level, and exceeded the historical level after 100 years.

Large snags increased above the current level on both FS/BLM lands and across the Basin *(fig. 2)*. Large snag abundance also reached or exceeded the historical level on FS/BLM-administered lands under all three alternatives. Across the Basin, large snags increased by 6 to 10 percent above the current level for all three alternatives, but remained about 75 percent of the historical amount. The major difference between alternatives was in the Dry Forest PVG where alternative S1 generated more mid-seral than late-seral forest. Alternatives S2 and S3 restored more late-seral forests in the Dry Forest PVG, consequently producing higher snag levels.

Small down wood increased very slightly on FS/BLM-administered lands under alternative S1, but decreased by several percent under S2 and S3 after 100 years *(fig. 4)*. Most of the declines were in the Dry Forest and Moist Forest PVGs where decreases in the amounts of mid-seral forest were roughly balanced by increases in the late-seral and early-seral stages. Alternatives S2 and S3 include management measures designed to decrease fuel loads. The declines in small down wood amounts largely reflected those effects. Small down wood amounts remained nearly constant, or increased slightly, for all three alternatives at the Basin level, reflecting less aggressive fuels reduction efforts on non-FS/BLM lands.

Large down wood amounts followed a pattern similar *(fig. 4)* to that of small down wood across the Basin. Amounts increased slightly on FS/BLM-administered lands under alternative S1, but decreased under alternatives S2 and S3. Fuel reduction efforts in both alternatives S2 and S3 should reduce large down wood amounts in actively managed areas. This trend should be offset to some degree by large increases in dense late seral forest in unroaded and wilderness areas, generating large down wood levels far above historical conditions in those areas. At the Basin scale, only alternative S2 resulted in a decline in large down wood, while alternatives S1 and S3 produced small increases. This also reflected the emphasis on fuel reduction on FS and BLM-administered lands under alternatives S2 and S3.

Conclusions

Small snag amounts have declined from the historical level on FS/BLM lands, but remained at roughly the historical level for the Basin as a whole. Large snag amounts have declined on both FS/BLM lands and across the Basin. Amounts of small and large down wood have increased beyond the historical levels on FS/BLM lands and across the Basin. Current amounts of snags and down wood have been influenced by four major processes:

- Forest succession;
- Timber (and firewood) harvest;
- Fire suppression with its impacts on stand composition and structure;
- Natural snag and down wood dynamics, including recruitment, fall rates, and rates of decay.

Our 100-year simulations indicated a long-term return to historical amounts for small snags on both FS/BLM-administered lands and across the Basin, due mostly to the succession of large areas of mid-seral stage forests to the late-seral stage. Large snags should return to historical levels on FS/BLM lands, but remain at roughly 75 percent of the historical amount across the Basin. Both small and large down wood amounts should remain above historical levels on FS/BLM lands and across the Basin. In this case, the dynamics are most influenced by the succession of large areas of mid-seral forest to late-seral forest and the long-lived nature of down wood itself. Increased prescribed fire will likely reduce the future accumulation of large down wood on FS/BLM lands, especially under alternative S2, but levels across the Basin under alternative S2 should approach those of historical conditions.

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Assessment of the Line Transect Method: An Examination of the Spatial Patterns of Down and Standing Dead Wood[1]

Duncan C. Lutes[2]

Abstract

The line transect method, its underlying assumptions, and the spatial patterning of down and standing pieces of dead wood were examined at the Tenderfoot Creek Experimental Forest in central Montana. The accuracy of the line transect method was not determined due to conflicting results of t-tests and ordinary least squares regression. In most instances down pieces were randomly distributed along transect segments. Down pieces generally had a clumped distribution of their directional orientation. Standing pieces were usually found to be randomly distributed within belt transects. Consistent clumping scale of down or standing pieces was not found when studied using the paired quadrat variance method.

Introduction

Coarse woody debris (CWD), principally logs and snags, plays a key role in a wide range of ecological processes in conifer forests. It is important for wildlife, plant regeneration, nutrient cycling, water quality, fire fuels and more (Harmon and others 1986, Maser and others 1979, Maser and others 1988).

A number of researchers have used the line transect method (Brown 1974, Howard and Ward 1972, Van Wagner 1968, Warren and Olsen 1964) for quantifying the down component of CWD. Most studies have assumed the accuracy of the line transect method when quantifying down debris. In a literature search for this paper, studies were not found that compared volume measured on a fixed area to the volume estimated on that same area with the line transect method, in the natural setting. Few studies have tested two important assumptions of the line transect method for large debris: random piece orientation and spatially random piece distribution.

Correcting for nonrandom piece orientation requires additional measurement effort in the form of additional transect lines or a mathematical correction. Identifying a random distribution may reduce the number of line segments and thus the effort required to reach some desired level of precision. If pieces are spatially clumped at some consistent scale on the forest floor, the identification of that scale

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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may be used to reduce or eliminate the bias introduced by nonrandom spatial distribution.

The objectives of this study were to 1) compare the volume of down debris (logs) measured on fixed-area plots against estimates of down debris made with the line transect method on the same area; 2) test two assumptions of the line transect method: pieces need to be distributed randomly in their orientation and at random, spatially, on the forest floor; 3) identify the spatial distribution of standing pieces (snags); and 4) examine for a consistent scale of clumping of down and standing pieces.

Methods

Study Site

This study was conducted at the Tenderfoot Creek Experimental Forest (TCEF) in central Montana *(fig. 1).* The forest extends in elevation from approximately 1900 to 2400 m and covers an area just less than 3,700 ha. Lodgepole pine *(Pinus contorta)* is the predominant cover type with scattered patches of subalpine fir *(Abies lasiocarpa)* and Engelmann spruce *(Picea engelmannii)* dominating older stands. Whitebark pine *(Pinus albicaulis)* and limber pine *(Pinus flexilis)* are also found throughout the TCEF.

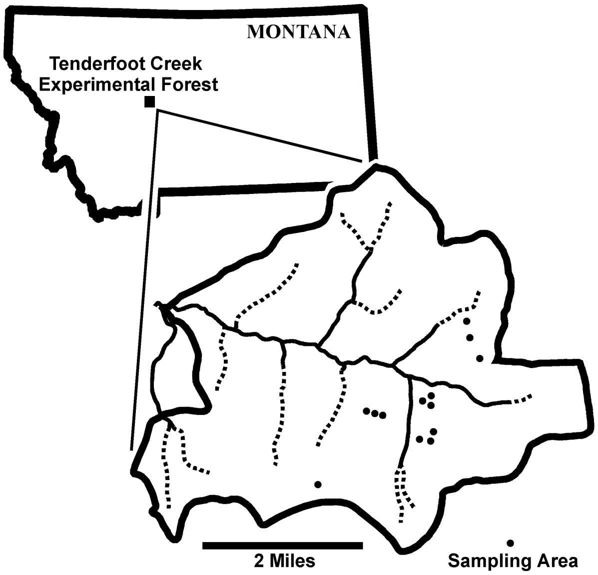

Figure 1—Study map of the Tenderfoot Creek Experimental Forest in central Montana, showing the locations of the13 sampling areas.

Sampling areas were established in five stands chosen from a fire history map of the TCEF (Barrett 1993). Four of the stands had last burned in 1873, 1845, 1765 and 1726, respectively. The fifth stand had burned in 1845 and again in 1873 (two-burn stand). None of the sampled stands showed any significant, identifiable sign of disturbance since the time of the last fire event. The 1873, 1845 and the two-burn stand were of the lodgepole pine cover type; the 1765 and 1726 stands were of the subalpine fir cover type. These stands were chosen because they were large enough to allow at least three sampling areas within each, had a wide variety of sizes and quantities of CWD, and were on sites with relatively little slope.

Field Sampling

Three sampling areas each were established in the 1873, 1845, 1765, and 1845 fire year stands. The two-burn stand had one sampling area. Each sampling area included ten 50-m line segments and ten 50 X 20-m belt transects. Line segments were oriented in the four cardinal directions. Belt transects were established by using the line segments as a centerline. Additionally, one 50 X 50-m (0.25 ha) fixed-area plot was established on five sampling areas *(fig. 2)*. The purpose of the fixed-area plots was to provide a "truth" to check the accuracy of line transect estimates of down debris.

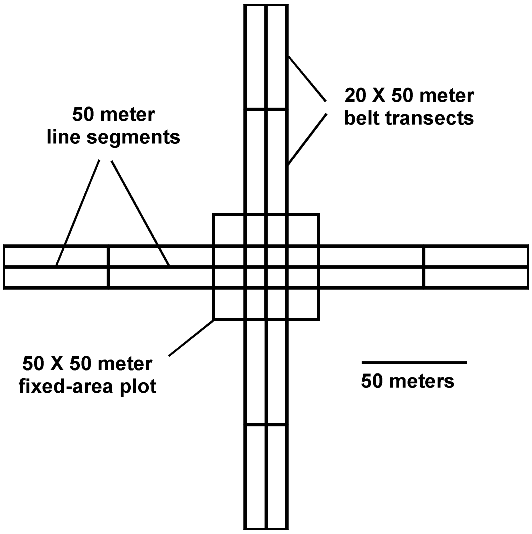

Figure 2—Sampling areas consisted of belt transects and 50-m line segments oriented perpendicularly. Five of the sampling areas had a 0.25-ha fixed-area plot that was positioned at the center of the sampling area.

Line-transect data in this study were used for three purposes: to provide a volume estimate for comparison with volume determined on a fixed area, to identify the log distribution pattern, and to examine clumping scale. Perpendicular lines were used to reduce or eliminate bias added by non-randomly-oriented pieces (Howard and Ward 1972). Estimated volumes were the mean of the 50-m north-south and east-west line segments.

Logs (down debris) in this study were defined as pieces leaning at an angle less than 45 degrees from the forest floor, ≥ 10 cm diameter—measured at the small end for pieces within the fixed-area plots or at the point of intersection for pieces measured with the line transect method—and at least 2 m long. Only pieces within 2 m of the forest floor were sampled. Diameter, directional orientation (large to small end), and distance from the start of the line segment were measured for all logs. Diameters of logs on the fixed-area plots were taken at three points: large end, mid-length, and small end. Diameters of logs recorded with the line transect method were measured at the point of intersection.

Some logs had decayed to the point where they were difficult to find, especially in areas of dense down debris, and therefore were extremely hard to quantify. For consistency, highly-decayed pieces were included in this study if they were above the plane of the ground surface, had no vegetation growing on them, and met the minimum log diameter and length criteria.

Measurements were collected for standing pieces (snags) if at least half of the area of the snag base fell within the 20 X 50-m belt. Snags were defined as pieces ≥ 10 cm diameter breast height (DBH), at least 2 m tall, and at an angle 45 degrees or greater from the forest floor. Distance from the start of the belt, measured perpendicular to the centerline of the belt, was recorded for each piece. Snags were the only component sampled using the belt transects.

Analysis

Logs and snags within the 0.25-ha fixed-area plot were mapped and measured. The volume of logs on each plot was calculated using Newton's formula (Avery and Burkhart 1983) and converted to a per-ha basis. Fixed-area volume was compared against the volume estimated by two perpendicular 50-m line segments run through the center of the fixed-area plot. Comparison of the measured, fixed-area volume and estimated, line-transect volume was made with t-tests and ordinary least squares (OLS) regression.

The volume of down woody debris on each 50-m line was estimated with the equation proposed by Van Wagner (1968):

$$v = \frac{\pi^2 \sum_{i=1}^{n} d_i^2}{8L} \tag{1}$$

in which d is diameter in cm, measured perpendicular to the length of the log, n is the number of individuals encountered, L is the length of line in meters, and v is the volume of down debris (m^3/ha).

Ordinary least squares analysis of fixed-area volume and line transect volume was accomplished by simultaneously testing that the intercept was equal to zero and the slope of the relationship was equal to one (Draper and Smith 1981). To test this hypothesis the Q-statistic was computed using:

$$Q = (\beta - b)' x' x (\beta - b) \tag{2}$$

in which β_0 and β_1 are the hypothesized population parameters (vector), b_1 and b_2 are the regression parameters (vector), and x′x is the matrix term of the independent variable (in this case the line-transect estimated volumes). The null hypothesis was rejected if the test statistic was greater than the critical value calculated with:

$$ps^2 F(p, v, 1-\alpha) \tag{3}$$

in which p equals the regression degrees of freedom, s^2 is the variance, and the F-value is from the appropriate F-statistic table.

Two popular tests were used to describe the pattern of piece distribution on the forest floor and the orientational distribution of logs. The first test used the variance:mean ratio (V/M test) as an indicator of spatial pattern. The second test, which will be referred to as the distribution test, compared the pooled frequency distribution against the frequency that would be expected given the Poisson and negative binomial distributions. The distribution test was used to identify orientational clumping.

Random piece distribution is an assumption of the line-transect method and was tested here with the V/M test. Each 250-m east-west and north-south line was divided into 10-m, 25-m, and 50-m segments, which resulted in a total of six tests per sampling area (two lines, three tests each). Snag distribution was also studied with the V/M test at the same three scales, within the belt transects. Tests were conducted at three segment lengths because clumps may appear at different scales. The segment lengths were chosen to be as long as possible while still allowing a sufficient sample size.

To test the spatial distribution of down pieces and snags with the V/M test (Ludwig and Reynolds 1988), the variance was calculated with the formula:

$$s^2 = \frac{\left(\sum_{x=0}^{k} \left(x^2 Fx \right) - \bar{x} n \right)}{N - 1} \tag{4}$$

in which k is the greatest frequency per sampling unit, x is the frequency class, Fx is the count in the x frequency class, n is the number of individuals, and N is the number of sampling units.

The chi-square test was used to check if the variance:mean ratio was significantly different from 1, where a value < 1 suggests uniform distribution and a value > 1 suggests clumped distribution. A random pattern is assumed when the variance:mean ratio is equal to 1. The snag data for three of the sampling areas were dropped from this analysis due to incomplete data.

It is important to note that the tests of log distribution using the line transect data were actually identifying the pattern of log crossings in one dimension, not in two dimensions on the forest floor. It is unclear whether the pattern identified by the V/M Test is indicative of the pattern of log distribution on the forest floor.

The distribution test was used to check for random directional orientation of logs. Logs were assigned to 1 of 36 classes by 10-degree increments and pooled by frequency. Pooling followed the recommendation of Ludwig and Reynolds (1988): when the number of frequency classes is less than five, the expected number in each class is not to be less than five; if the number of classes is five or greater, then the expected number is not to be less than three. Then the frequency distribution of the pooled data was tested against the Poisson and negative binomial distributions of expected counts using the chi-square test. On two of the sampling areas, counts within each frequency class were pooled to three individuals per class instead of the five per class recommended by Ludwig and Reynolds (1988) because of the low number of down pieces. The data for one sampling area were not analyzed for orientation due to degrees of freedom limitations.

Two hypotheses were tested with the distribution test: the frequency distribution followed the Poisson distribution (random distribution); the frequency distribution followed the negative binomial distribution (clumped distribution). Rejecting the first hypothesis and failing to reject the second implied a clumped pattern.

The paired quadrat variance (PQV) technique (Ludwig and Reynolds 1988) was used to identify any consistent clumping scale. A peak in the graph of variance vs. quadrat spacing indicated clumps occurring at about twice the quadrat spacing (block) distance. To accomplish the test, a 5-m line segment was chosen to serve as a "quadrat" and the variance was calculated using the equation:

(5)

$$\operatorname{var}(x_s) = [\frac{1}{N-S}]\{[0.5(x_1 - x_{1+s})^2] + [0.5(x_{1+s} - x_{(1+s)+s})^2] + \ldots + [0.5(x_{N-s} - x_N)^2]\}$$

in which S is the spacing (in m) between quadrats, s is the quadrat sequence number, N is the number of quadrats, and x is the piece count in the quadrat. The variance was calculated to a block spacing of N/2 for each north-south and each east-west line in the study. Ludwig and Reynolds (1988) suggest using N/10 as the maximum quadrat spacing; however, N/2 was used to extend the analysis to a larger area. This may have resulted in some unreliable variance estimates at the larger quadrat spacings. By convention, an error level of p = 0.05 was used throughout this study.

Results and Discussion

Fixed-Area/Line Transect Volume Comparison

The accuracy of the line-transect method was tested with t-tests and OLS regression on the 0.25-ha fixed-area plots. T-tests indicated that there was no significant difference between the mean volume estimated by two 50-m line segments and the volume measured on the fixed-area plots using Newton's formula, except on sampling area 221 *(table 1)*. Down pieces were not measured with the line-transect method on sampling area 221; thus, the result may be an indication of the estimating power of the line-transect method on lightly loaded areas. Brown (1974) and Pickford and Hazard (1978) note that coefficient of variation decreases as sample size increases, and they suggest counting at least 25 pieces for dependable results.

Table 1—*T-test results of total fixed-area volume compared against the mean volume estimated with two perpendicular 50-m lines found no significant differences, except on sampling area 221 where no pieces were measured using the line transect method.*

Plot	F/A[1] vol.	L/T[1] vol.	L/T std. dev.	t	p(t)
	------------------------m^3/ha	-------------------			
001	14.91	33.23	4.26	6.08	0.10
002	134.52	139.83	77.78	0.09	0.94
221	7.74	0.0	0.0	-	-
248	277.47	294.18	11.71	2.01	0.29
280	33.08	24.88	3.19	3.63	0.17

[1] F/A = fixed-area; L/T = line transect

Ordinary least squares regression of two, 50-m line segments and fixed-area volumes resulted in a significant (F = 368.76; p = (368.76) = 0.0003) and highly correlated ($r^2 = 0.99$) relationship *(fig. 3)*. However, the Q-statistic was greater than the critical value (62895.66 > 1093.12), which indicated that β_0 was significantly different from 0 and/or β_1 was significantly different than 1. Because of the small sample size, inconsistent t-test and Q-test results, and inconsistent tests of the underlying assumptions of the line transect method, the ability of the line-transect method to estimate down volume was not determined.

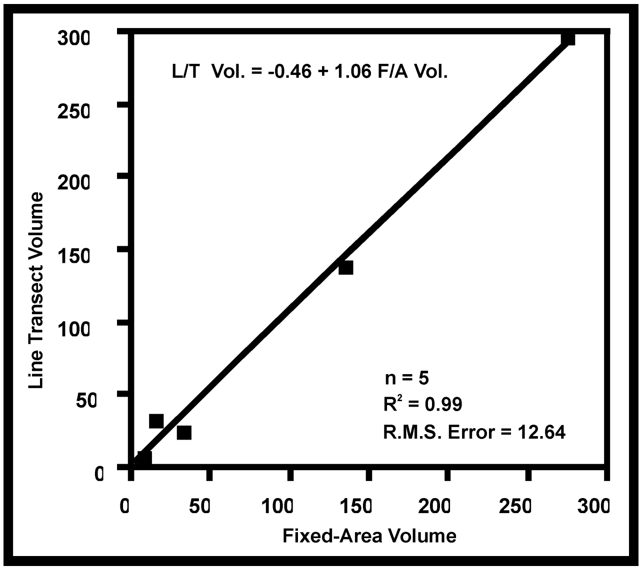

Figure 3—Ordinary least squares regression results of volume estimated with two perpendicular 50-m line segments vs. the actual volume measured on a 0.25-ha fixed-area plot.

Log Distribution

The V/M test was used to identify the spatial distribution of logs on the forest floor *(table 2)*. Of 78 tests performed on the line-transect data, 18 (23 percent) tested as having a clumped log distribution. The remaining 60 (77 percent) tested as having a random distribution. No lines were found to have a uniform distribution of logs.

Table 2—*Log distribution indicated by the V/M Test indicated a generally random pattern at the three scales tested.*

	Scale		
Pattern	**10 m**	**25 m**	**50 m**
	---------------------Number of sampling areas-------		
Uniform	0	0	0
Random	20	22	18
Clumped	6	4	8

In some cases the log distribution pattern changed with the scale of the test data. Six of the 13 sampling areas had at least one test indicating a clumped distribution. One sampling area had five of the six tests indicate a clumped distribution. Every sampling area had at least one test that indicated a random pattern. Six sampling areas did not test for a clumped pattern at any scale. An identifiable relationship was not found between the number of individuals, whole line or per segment, and clumped pattern. A relationship was not found between segment length (scale) and clumped pattern.

On sampling areas in the youngest stand (1873), the low number of logs may have led to unreliable estimates of the variance: mean ratio and thus the indicated pattern. For the remainder of the sites, however, the V/M method seemed to be appropriate.

Log Orientation

There was an obvious eastward directional bias when down pieces from all sampling areas were graphed together *(fig. 4)*. Log orientation data were tested separately for each sampling area. Only five sampling areas had pieces that followed the Poisson distribution. Log orientation followed the negative binomial distribution on 12 of the sampling areas (The low number of down pieces on one sampling area did not allow testing against the negative binomial distribution.) This indicated that in eight of 12 instances there was evidence of clumped log orientation.

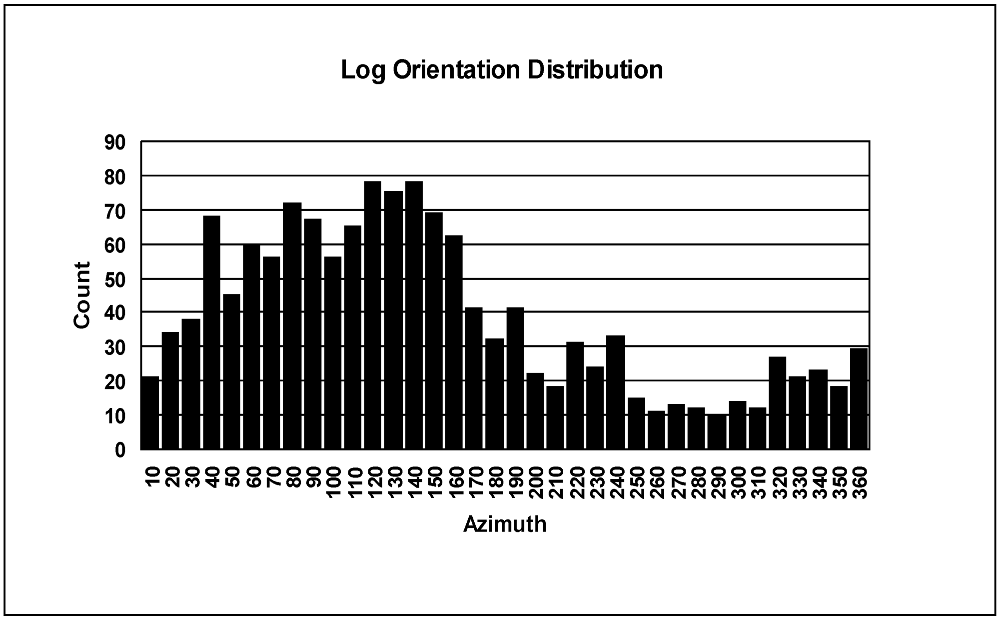

Figure 4—Log orientation of all sample pieces showed an obvious eastward bias.

Effects of Scale on CWD Estimates

The PQV model revealed little evidence of a consistent scale effect on CWD estimates. The graphs of variance vs. quadrat spacing for sampling areas 3 and 398 indicate peaks of variation at some block sizes, but whether these indicate clumps or simply the random distribution of logs is unclear *(fig. 5)*. Results of the V/M test only confounded any analysis. There was no systematic pattern to the graphs of variance for any of the 13 sampling areas in this study.

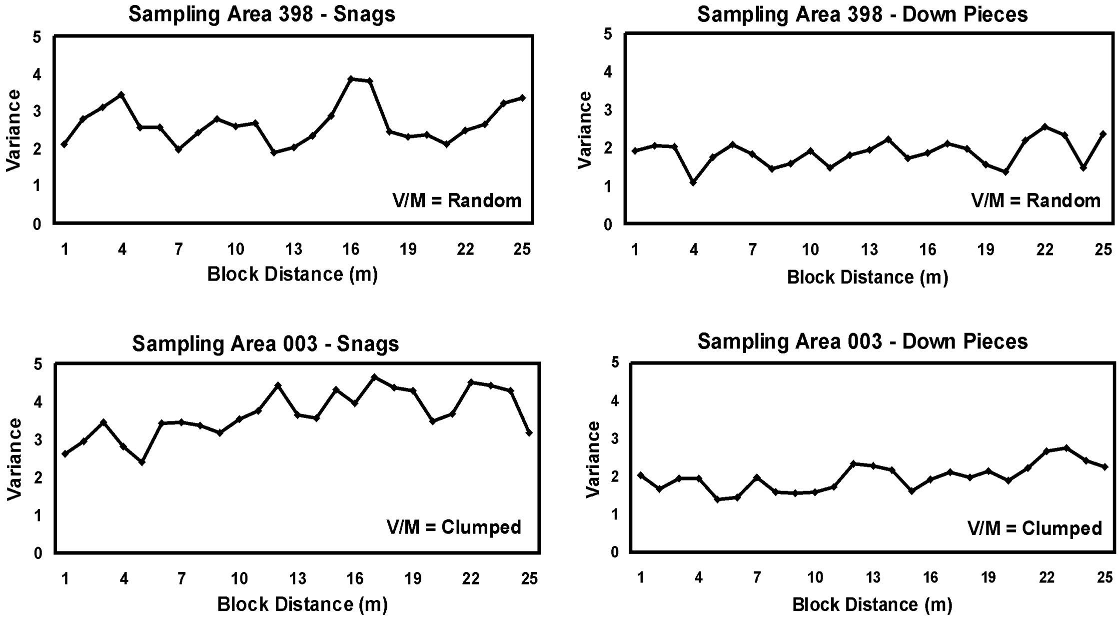

Figure 5—A consistent pattern of down or standing piece distribution was not identified using the paired quadrat variance method. Four examples of the original 46 graphs are presented here for the reader's examination.

Snag Distribution

Like logs, snags showed only moderate evidence of clumped distribution *(table 3)*. Of 60 tests, 37 (62 percent) indicated snags were randomly distributed. Twenty-two (37 percent) indicated a clumped distribution of snags and one test indicated a uniform distribution. Six of the 20 belts were found to have a clumped distribution of snags at each of the three scales. Half of the belts were found to have clumped snags at at least one scale, and nine tests indicated snags were distributed randomly at every scale. Only one sampling area tested as having a clumped distribution on both lines at every scale. A relationship was not found between the number of individuals and the distribution suggested by the V/M test. An identifiable relationship was not found between scale and distribution.

Table 3—*Snag distribution indicated by the V/M test indicated a generally random pattern at the three scales tested.*

Pattern	Scale 10 m	25 m	50 m
	------------Number of sampling areas-------		
Uniform	0	1	0
Random	12	12	13
Clumped	8	7	7

Conclusion

The accuracy of the line transect method could not be determined in this study for two reasons: inconsistent test results indicated that two important assumptions of the line transect method, random spatial and orientational distribution, could not be guaranteed; and the sample size was quite small (n = 5).

The bias introduced by not meeting the assumptions of the line transect method was probably small, however. First, the sampling scheme used in this study (perpendicular lines) should have substantially reduced any bias introduced by clumped log orientation (Howard and Ward 1972). Secondly, because log distribution was found to be generally random at the scales tested in this study (10-m, 25-m and 50-m) there was likely little bias introduced by clumped pieces.

Most tests of log and snag distribution indicated a random pattern. Because tree regeneration and mortality are generally assumed to occur in aggregated patterns (Franklin and others 1987, Harmon and others 1986, Lundquist 1995, Maser and others 1988), the results from this study were somewhat surprising. However, lodgepole pine tends to regenerate in a relatively uniform manner (Fischer and Bradley 1987) with tree mortality and log accumulation possibly following that pattern. Lodgepole pine comprised some or all of the tree cover on the sampling areas in this study, which may explain finding mostly random patterns. Also, the scale of sampling may have had an effect on the results because the line segment and quadrat sizes tested for log and snag distributions were quite small.

The eastward bias of down pieces was likely not due to logs moving to new orientations after they fell, since the sampling areas had no or little slope (less than 15 percent). Also, pieces were probably not greatly affected by wind events exacerbated by local geography (ridge-tops, canyons, etc.) but simply fell away from the prevailing westerly winds.

The usefulness of the PQV method was not demonstrated here theoretically due to the relatively small quadrat distance tested. The method may prove useful for variance and block size relationships over a larger area—1 or 2 ha for example. However, the potential effects of disturbance, ridge-tops, differing stand ages, steep slopes, and changing aspects on the pattern of piece distribution must be considered.

Acknowledgments

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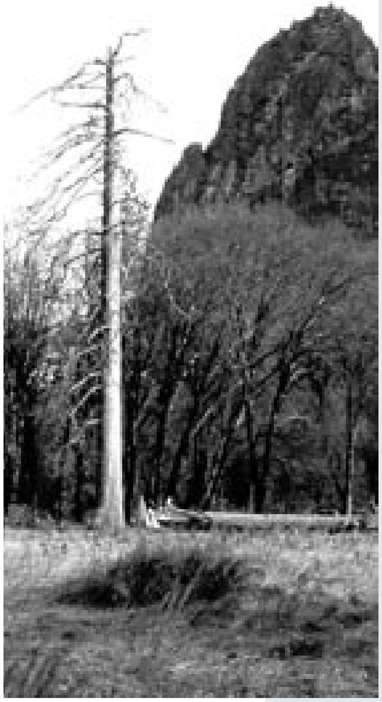
Management of Dead Wood



Forest Management and the Dead Wood Resource in Ponderosa Pine Forests: Effects on Small Mammals[1]

Carol L. Chambers[2]

Abstract

Changes in vegetation structure and composition affect habitat for wildlife. Species such as small mammals that are restricted to small home ranges and are relatively immobile may be most affected since it is more difficult to find and move to new habitat. In the southwestern United States, forest management treatments (thinning and prescribed burning) are being implemented to alter structure and function of ponderosa pine *(Pinus ponderosa)* ecosystems and recreate pre-settlement (ca. 1870) tree species composition and size class distribution. These forest restoration treatments will affect the availability of dead wood to wildlife (e.g., prescribed fires may consume dead wood, forest operations may create snags and logs). I live-trapped small mammals in a northern Arizona ponderosa pine forest prior to restoration treatment and found that mouse species (*Peromyscus* species) were associated with some dead wood elements (e.g., Gambel oak *[Quercus gambelii]* snags, ponderosa pine snags, ponderosa pine stumps).

Introduction

Standing dead trees and logs are important components of wildlife habitat. They provide nesting, roosting, feeding, loafing, and storage sites for over 75 species of birds, mammals, reptiles, and amphibians in the Southwest (Degenhardt and others 1996, Rabe 1998, Scott 1979, Scott and Patton 1989). Many of these animals have important ecological roles, such as dispersing seeds and mychorrhizal fungi, helping to control insect populations, and serving as prey for other species (Bergvinson and Borden 1992, Maser and others 1988, Peterson 1980, Ward and Block 1995).

Vertebrate population densities may change in response to change in vegetation structure and composition (see for example, Chambers and others 1999, Scott 1979, Szaro and Balda 1986). Although some wildlife species (birds, large ungulates) are highly mobile and can move to more favorable habitat (assuming it is unoccupied), many species (small mammals, reptiles, amphibians) are often restricted to relatively small areas (i.e., 2 to 20 ha per individual or population) (e.g., Hall and Morrison 1997). Forest management practices may have differential effects on vertebrate populations depending on the scale at which the treatments are applied and the size of habitat used by an organism.

Ponderosa pine forests cover about 3.2 million ha in Arizona and New Mexico (Klemmedson and Smith 1979). These forests appear to be at increasing risk of

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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catastrophic fire as a result of 130 years of Euro-American influence. A combination of fire suppression, logging practices, insect infestations, livestock grazing, and a shift towards a warmer and wetter climate has altered the composition of ponderosa pine forests (Cochran and Hopkins 1991, Cooper 1960, Covington and Moore 1994, Grissino-Mayer and Swetnam 2000, Touchan and others 1996). Livestock grazing reduced native grasses and other fine fuels that spread low intensity fires. Grazing also exposed bare mineral soil, which allowed establishment of ponderosa pine seedlings in years following high cone production (Klemmedson and Smith 1979, Touchan and others 1996). Fire suppression has resulted in greater survival of young trees, contributing to forest densities of >3,000 trees/ha in the 1990s compared to 60 trees/ha in 1876 (Mast and others 1999).

Ecological restoration, using silvicultural tools such as thinning and prescribed burning, may help reestablish structure and function of indigenous ecosystems by recreating pre-settlement (ca. 1870) tree species composition and size class distribution and reestablishing a frequent, low intensity fire regime (Covington and others 1997). However, restoration treatments will affect the availability of dead wood to wildlife. Thinning and pruning may increase log and slash densities. Slash treatments that leave piles or windrows increase habitat for some vertebrates (e.g., small mammals, Goodwin and Hungerford 1979). Prescribed fire may increase or decrease the dead wood resource. Boucher and others (1999), Gaines and others (1958), and Gordon (1996) found that prescribed fire created dead wood; however, live trees killed by fire were predominantly small in diameter and therefore not effective replacements of large logs and snags. Prescribed fires will also incinerate existing snags and logs, removing up to 50 percent of ponderosa pine snags and 60 percent of logs (Gaines and others 1958, Gordon 1996, Horton and Mannan 1986, Randall-Parker and Miller 2002). In addition, Horton and Mannan (1988) found that large (>30 cm dbh) and more decayed ponderosa pine snags were more flammable, and therefore more likely to be lost. This loss of large dead wood may be particularly detrimental to wildlife, because cavity nesters (birds and bats) select larger snags (≥46 cm diameter), large snags persist longer than small snags (Neitro and others 1985, Rabe and others 1998, Scott and Oldemeyer 1983), and replacement of large snags may take a long time (e.g., ≥200 years for a ponderosa pine to reach 46 cm dbh under normal stocking, site index 70 [Meyer 1961]). Large snags are often the origin of large logs, so fires may have both immediate and long-term impacts on both standing dead and down wood.

If not incinerated, snags and logs may be altered by fire and their usefulness as wildlife habitat decreased (Gaines and others 1958, Gordon 1996). After a prescribed burn, Gordon (1996) suggested that the utility as habitat of >70 percent of logs in her study was decreased, because logs were charred and case-hardened, making them more difficult for animals to excavate. Most snags fell (50 percent, Gordon 1996), at which point they were considered useful as log habitat. Additional fires might further reduce available dead wood.

What do we know specifically about use of dead wood in the Southwest? I found 41 articles *(table 1)* that described either dynamics of dead wood or use of dead wood as habitat for wildlife in the Southwest. The literature generally focused on ponderosa pine ecosystems (n = 32), although five papers described mixed conifer ecosystems and four papers described dead wood in both forest types. Snag dynamics or use was the most common topic discussed (n = 33). Of these, 11 papers described use of snags by primary or secondary cavity-nesting birds and 10 described other types of use by wildlife. The remaining 12 papers described snag recruitment and longevity, pre-settlement forest conditions in the Southwest, or effects of prescribed fire on dead wood. Fifteen papers discussed dynamics (n = 6) or wildlife use (n = 9) of logs.

Of the 41 papers discussing dead wood in the Southwest, only 4 (Goodwin and Hungerford 1979, Kyle 2000, Smith and Mannan 1994, Ward and Block 1995) described small mammal use of down wood in ponderosa pine forests. I examined small mammal use of ponderosa pine stands in northern Arizona. My objective was to determine how the availability of standing and down wood and other habitat elements affected abundance of small mammals. The study was conducted in areas scheduled for forest restoration treatments (thinning, prescribed burning). From these data, I have speculated on how restoration may affect dead wood and impact small mammal communities. Following restoration treatments, stands will be resampled and pre- and post-treatment comparisons made.

Table 1—*Dead wood (snags and logs) in the Southwest reference list.*

Author(s)	Year	Snags	Logs	Wildlife
Mixed conifer				
Vahle and Patton	1983		X	X
Conway and Martin	1993	X		X
Franzreb	1978	X		X
Franzreb and Ohmart	1978	X		X
Li and Martin	1991	X		X
Ponderosa pine				
Goodwin and Hungerford	1979		X	X
Smith and Mannan	1994		X	X
Ward and Block	1995		X	X
Smith	1996		X	X
Covington and Sackett	1984		X	
Graham and others	1994		X	
Balda and others	1983	X		X
Crocker-Bedford	1993	X		X
Cunningham and others	1980	X		X
Dwyer	2000	X		X
Hay and Guntert	1983	X		X
Horton and Mannan	1988	X		X
Keller	1992	X		X
Rabe and others	1998	X		X
Reynolds and others	1992	X		X
Scott	1978	X		X
Scott	1979	X		X
Szaro and Balda	1986	X		X
Brawn and Balda	1988	X		X
Ffolliot	1983	X		
Mast and others	1999	X		
Miller and Benedict	1994	X		
Pearson	1937	X		
Scott and Oldemeyer	1983	X		
Wadsworth	1943	X		

(table 1 **continued)**

Author(s)	**Year**	**Snags**	**Logs**	**Wildlife**
Block and Finch	1997	X	X	X
Germaine	1999	X	X	X
Kyle	2000	X	X	X
Covington and Moore	1994	X	X	
Covington and others	1997	X	X	
Gaines and others	1958	X	X	
Gordon	1996	X	X	
Mixed conifer and ponderosa pine				
Mollohan and others	1989		X	X
Balda	1975	X		X
Dahms and Geils	1997	X		
Ganey	1999	X		

Methods

Study Area

I live-trapped small mammals at Mt. Trumbull, in the Arizona Strip north of the Colorado River, in northern Arizona (latitude 36° 22’ 0”, longitude 113° 11’ 0”). The study area ranged from 2,055 to 2,277 m in elevation. Tree density averaged 1,642 trees per ha, with ponderosa pine dominating (ponderosa pine averaged 90 percent of stand basal area). Gambel oak, pinyon pine *(Pinus edulis),* Utah juniper *(Juniperus osteosperma),* and New Mexican locust *(Robinia neomexicana)* comprised the remaining 10 percent basal area. Log density averaged 6.4/ha, 51.0, 1.6, 107.6, respectively, for large (>50 cm diameter) and small ($\leq$50 cm) ponderosa pine logs; large (>15 cm diameter) and small ($\leq$15 cm) Gambel oak logs. Snag density averaged 1.6/ha, 40.3, 7.8, and 216.6, respectively, for large and small ponderosa pine snags; large and small Gambel oak snags.

Small Mammal and Habitat Sampling

I established trapping grids within five 32-ha experimental restoration units. Each unit consisted of two stands: one treatment and one control, approximately equal in size. Treatment stands were to be harvested in 1999; I sampled all stands prior to harvest in July 1998.

I established a 10 x 10 trapping grid (4 ha grid) centered in each 16-ha stand (n = 10 grids). Grid points were placed 20 m apart. At each point on the trapping grid, I placed one Sherman live trap (8 x 8 x 23 cm). Traps were baited with a peanut heart and seed mix. Traps were set for four to five consecutive nights (until recapture rates were >80 percent) and checked daily. Traps were closed during the day to prevent capture of diurnal animals and reopened approximately 1 hour before dusk.

Units 1, 2, and 3 were sampled July 11-15, 1998. Units 4 and 5 were sampled July 26-29, 1998. All animals were weighed, measured (total body length, lengths of tail, ear, and right hind foot), ear-tagged with a unique number, and released at the point of capture.

I obtained vegetation and habitat data for each stand from the Northern Arizona University School of Forestry Ecological Restoration Institute. These data were collected June through August 1998 for a subset of trap stations (12 to 16 trap stations systematically distributed in each grid to equally sample throughout the trapping grid). Overstory data (tree density, basal area, canopy cover, snags, logs, stumps) were measured on a 0.04 ha plot and shrubs were measured on a 0.01 ha plot centered on each trap station location *(table 2)*. Other understory habitat features (grasses, forbs, mosses, lichens) were measured by point intercept along a 50-m line transect (166 points per transect) and their frequency per trap station calculated *(table 2)*.

Table 2—*Habitat variables used in developing habitat relationships models for small mammal species (deer mouse, pinyon mouse, brush mouse) at Mt. Trumbull, Arizona, June–August 1998.*

Variable	Definition
Understory	
Lichen	Percentage of lichen and moss cover
Litter	Percentage of litter cover
Forb	Percentage of forb cover
Grass	Percentage of grass cover
Shrub	Percentage of woody plant (shrubs and trees <1.4 m) cover
Logs	Number of logs > 0.15 m long by species (ponderosa pine, Gambel oak, New Mexican locust, Utah juniper) and size class (for ponderosa pine: small ≤50 cm diameter, large >50 cm diameter; for Gambel oak, small ≤15 cm diameter, large >15 cm diameter; size classes were not created for New Mexican locust or Utah juniper)
Stumps	Number of stumps by species (ponderosa pine, Gambel oak, New Mexican locust, Utah juniper) and size class (for ponderosa pine: small ≤50 cm diameter, large >50 cm diameter; for Gambel oak, small ≤15 cm diameter, large >15 cm diameter; size classes were not created for New Mexican locust or Utah juniper)
Overstory	
Basal area	Basal area (m^2/ha) for all live trees combined and for each tree species (ponderosa pine, Gambel oak, New Mexican locust, Utah juniper, pinyon pine)
Live trees	Number of live trees by species (ponderosa pine, Gambel oak, New Mexican locust, Utah juniper) and size class (for ponderosa pine: small ≤50 cm diameter, large >50 cm diameter; for Gambel oak, small ≤15 cm diameter, large >15 cm diameter; size classes were not created for New Mexican locust, or Utah juniper) and decay condition (1 = live tree, no sign of decay, 2 = live tree, declining, some evidence of decay (e.g., dead branches)
Snags	Number of snags by species (ponderosa pine, Gambel oak, New Mexican locust, Utah juniper), size class (for ponderosa pine: small ≤50 cm diameter, large >50 cm diameter; for Gambel oak, small ≤15 cm diameter, large >15 cm diameter; size classes were not created for New Mexican locust, or Utah juniper), and decay condition (3 = recent snag, 4 = loose bark snag, 5 = snag without bark remaining, 6 = snag broken above 1.4 m)

Live trees and snags or partial snags were classified into decay classes. Decay class 1 was a live tree with no evidence of dead branches. Decay class 2 was a live tree with dead branches (declining), decay class 3 was a recent snag, decay class 4 was a snag with loose bark, decay class 5 was a snag with no bark remaining.

Statistical Analyses

Stand-Level Analyses

I calculated capture rates per stand (number of animals per 100 trap nights [TN]) *(table 3)* for each *Peromyscus* species. I averaged overstory and understory variables for each stand. Habitat variables that were not normally distributed or with unequal variance were transformed by taking the square root of the variable or by using $\log_{10}$(variable + 1) (Sabin and Stafford 1990).

I reduced the number of habitat variables for multiple linear regression to adjust for small sample sizes. For each mouse species, I developed models using subsets of ≤ 3 habitat variables. I used Spearman correlations to determine univariate relationships between each species of *Peromyscus* and habitat variables that were selected in multivariate models (SAS Institute Inc. 1985) (Spearman correlations: $R > 0.6$, $P \leq 0.05$ for deer mouse, $R > 0.5$, $P \leq 0.1$ for brush mice, and $R > 0.7$, $P \leq 0.03$ for pinyon mice).

I used stepwise linear regression analysis to identify habitat variables that, in combination, were associated with small mammal capture rates (Sokal and Rohlf 1981, SAS Institute Inc. 1985). I used Akaike's Information Criterion (AIC) to select models with predictive power that used the fewest variables; low AIC values are associated with models that give the best fit of data. To select the best model, I compared AICd values (relative AIC value for each model, calculated by taking the difference between the model with lowest AIC value). If AICd values were < 4, models were assumed equally effective in predicting presence of the animal species and the most parsimonious model selected (Burnham and Anderson 1998:43-48).

Table 3—*Capture rates (number of animals per 100 trap nights [TN]) for deer mouse* (Peromyscus maniculatus), *brush mouse* (P. boylii), *and pinyon mouse* (P. truei) *at Mt. Trumbull, Arizona, July 1998. For stand, C represents the control unit (will not be thinned or burned) and T represents the treatment unit (untreated at the time of data collection).*

	Capture Rate (number/100 TN)		
Stand	**Deer Mouse**	**Brush Mouse**	**Pinyon Mouse**
1C	3.0	4.8	0.0
1T	3.6	5.8	0.6
2C	4.4	0.0	0.4
2T	12.0	1.0	0.0
3C	2.6	0.0	0.0
3T	2.6	0.2	1.2
4C	1.3	0.0	4.8
4T	0.8	0.5	5.0
5C	0.3	0.0	3.8
5T	0.5	0.8	2.8

Trap Station Analyses

I averaged values for each habitat variable by trap station and used these data to develop habitat association models. I used logistic regression as a means of selecting variables that separated trap stations used by small mammals from unused trap stations. I conducted separate analyses for each mouse species (deer mouse, brush mouse, pinyon mouse). I used the Hosmer and Lemeshow goodness-of-fit test to determine whether the distribution of probabilities produced by my model(s) fit the logistic probability distribution (SAS Institute, Inc. 1990).

Results

I captured 270 individuals of 3 species during the trapping period: 135 deer mice (50 percent of captures), 74 pinyon mice (27 percent of captures), and 61 brush mice (23 percent of captures). Deer mice were more abundant in units 1, 2, and 3. Brush mice were most abundant in unit 1. Pinyon mice were most abundant in units 4 and 5 *(table 3).*

Stand-Level Analyses

Models with two regressors were strongest predictors of deer mouse and pinyon mouse habitat use based on AICd values. For brush mouse, there was no difference between the 1- and 2-variable models based on AICd values *(table 4).*

Large Gambel oak trees and small ponderosa pine snags explained 87 percent of the variation in deer mouse abundance (F = 24.3, df = 2, 9, $P < 0.0007$). Deer mice were positively correlated with large Gambel oaks (R = 0.64, $P = 0.05$) *(fig. 1A)* and negatively correlated with small ponderosa pine snags (R = -0.74, $P = 0.01$) *(fig. 1B).*

Table 4—*Stepwise linear regression models developed to explain differences in habitat use at the stand level by deer mice, brush mice, and pinyon mice, Mt. Trumbull, Arizona, 1998.*[1]

Species	Habitat Variable	Partial R^2	Model R^2	AIC	AICd
Deer mouse	>15 cm dbh Gambel oak trees	0.62	0.62	18.0	9.2
	<50 cm dia. ponderosa pine snags	0.26	0.87	**8.8**	0
Brush mouse	>50 cm dia. ponderosa pine stumps	0.37	0.37	13.5	2.6
	Lichen and moss cover	0.23	0.61	10.9	0
Pinyon mouse	Juniper species basal area	0.90	0.90	-6.1	4.9
	Ponderosa pine basal area	0.05	0.95	**-10.9**	0

[1] Akaike's Information Criterion (AIC) was used to select models with predictive power using fewest variables; lowest AIC values are associated with models that give the best fit of data (best model is depicted in bold typeface, if not indicated in bold typeface, either model is equally acceptable). AICd is the relative AIC value for each model, calculated by taking the difference between the model with lowest AIC value.

Basal area of juniper and ponderosa pine trees explained 95 percent of the variation in pinyon mouse abundance (F = 67.2, df = 2, 9, P = 0.0001) *(table 4).* Pinyon mice were positively correlated with juniper basal area (R = 0.85, *P* = 0.002) *(fig. 1C)* and ponderosa pine basal area (R = 0.71, P = 0.02) *(fig. 1D).*

Large ponderosa pine stumps explained 37 percent of the variation in brush mouse abundance (F = 4.8, df = 1, 9, *P* = 0.06) *(table 4).* Brush mice abundance was negatively correlated with large ponderosa pine stump density (R = -0.61, *P* = 0.06) *(fig. 1E).* Lichen cover was not significantly correlated with brush mouse abundance (R = 0.15, *P* = 0.7), and it did little to explain more variation in mouse abundance (based on AICd values) when included in the multiple regression model *(table 4)* (F = 5.4, df = 2, 9, *P* = 0.04).

Trap Station Analyses

Of 143 trap stations with vegetation data, I captured deer mice at 14 stations, pinyon mice at 12 stations, and brush mice at 6 stations. Combining all species, I captured mice at 29 of 143 trap stations.

Trap stations with the highest probability of deer mice capture had higher forb cover, higher live tree basal area, and higher densities of small (<15 cm dbh) Gambel oak live trees or recent snags (decay class 2 or 3). Pinyon mice were captured at trap stations with higher pinyon pine basal area, small (<15 cm dbh) Gambel oak trees, and <50 cm diameter ponderosa pine stumps. There was a higher probability of brush mouse capture at trap stations with lichen cover, >50 cm dbh ponderosa pines, and <15 cm dbh Gambel oak trees or recent snags (decay class 2 or 3).

Discussion

Habitat Associations of Small Mammals

The deer mouse is one of the most widespread rodents. In the Southwest, it is common in forest types from high elevation spruce/fir *(Picea/Abies)* forests to ponderosa pine forests. Pinyon and brush mice are more selective of habitat. Brush mice occur in areas with dense rock and shrub cover, usually in pinyon-juniper, riparian, oak, and pine-oak woodlands (Goodwin and Hungerford 1979, Ward and Block 1995). Pinyon mice occur in pinyon-juniper and xeric oak woodlands (Cranford 1982, Morrison and Hall 1998).

Ward and Block (1995) described habitat associations of deer mice in ponderosa pine/Gambel oak forests of northern Arizona. They found that deer mice used more open sites with less shrub and midstory canopy, and smaller densities of Gambel oak. They also found deer mice used sites with more slash piles and greater litter depth. Goodwin and Hungerford (1979) found that deer mice were correlated with stump and log density. They found that mice hid in larger logs or stumps, fallen logs created spaces for nesting, and that mice also nested inside bark that had separated from stumps and logs. At the stand level, I found deer mice were more abundant in areas with higher densities of large Gambel oak. Deer mice were less abundant in stands with high densities of small ponderosa pine snags. Small ponderosa pine snags were correlated with high densities of live ponderosa pine (R = 0.71, *P* = 0.02); deer mice were therefore less abundant in dense ponderosa pine stands. At the trap station level, deer mice were more abundant in areas with high forb cover and live tree basal area.

Gambel oak was an important predictor of deer mouse density. Because deer mice are generalists positively correlated with Gambel oak and negatively correlated with high densities of ponderosa pine, I hypothesize that deer mice will continue to increase in density in treated units for several years following treatment; then populations will stabilize.

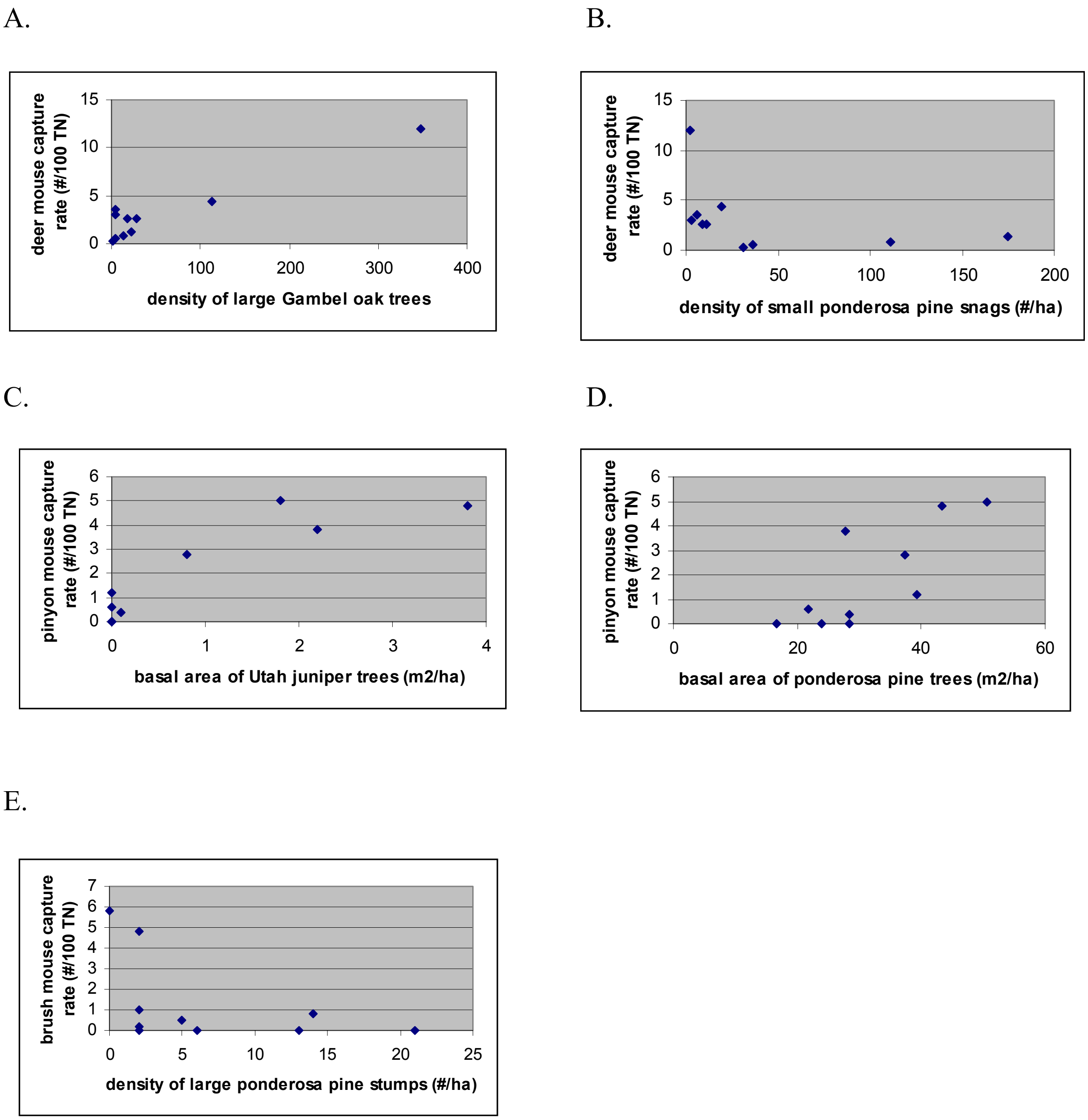

Figure 1—Spearman correlations for habitat variables that were used in multiple linear regression models for deer mouse (A and B), pinyon mouse (C and D), and brush mouse (E). Capture rate is standardized as number of individuals captured per 100 trap nights (#/100 TN). Large Gambel oak were >15 cm diameter. Small ponderosa pine snags were ≤50 cm dbh; large ponderosa pine stumps were >50 cm diameter.

Ward and Block (1995) found brush mice more abundant in areas with steeper slopes, low vegetation cover, sparse tree canopy cover, greater Gambel oak basal area, greater Gambel oak tree and shrub density, greater log volume, and less ponderosa pine basal area. Goodwin and Hungerford (1979) found high densities of brush mice along rocky slopes. These animals used windrowed slash piles. Goodwin and Hungerford (1979) also found that brush mice were much less abundant in areas of pure ponderosa pine or in mixed pine-juniper forest. I found few correlations between brush mice and habitat variables. The regression model I developed for brush mice explained less variation than models developed for pinyon and deer mice. Brush mice were negatively correlated with large ponderosa pine stump density. Brush mice were captured most frequently at Mt. Trumbull in an area with rocky basalt-derived soils adjacent to a recent (~6,000 BP) lava flow. I found large ponderosa pine stumps were negatively correlated with large ponderosa pine trees ($R = -0.55$, $P = 0.10$), which may indicate that brush mice were using more open sites. Lichen cover (likely an indicator of rock cover), large ponderosa pine and small Gambel oak trees were predictors of brush mouse habitat at the trap-station level, indicating their use of more open, brushy, rocky habitats. I hypothesize that brush mice populations will remain stable or slightly increase following harvest treatment since they are less reliant on overstory cover but use shrub and rock cover for habitat. Shrubs will likely increase on treated units; rock cover will not change.

I found no studies that documented habitat use of pinyon mice in ponderosa pine forests. I found that pinyon mice were associated with Utah juniper and ponderosa pine basal area. Pinyon mice were captured most frequently in stands with high densities of small diameter trees. These sites were lower in elevation, with higher densities of Utah juniper and pinyon pine. At the trap-station level, pinyon mice were captured in areas with high pinyon pine density, and high abundance of small Gambel oak trees and small ponderosa pine stumps. Suppression mortality may have resulted in high densities of small logs on the forest floor in these stands, but high densities of down wood may not necessarily be the cause of pinyon mouse habitat use. Other factors, such as the presence of pinyon pine and Utah juniper, may have been more important influences in use of habitat by pinyon mice. I hypothesize that pinyon mice populations will decline following harvest since pinyon mice are associated with high density of small diameter trees.

I found associations between habitat elements and relative abundance for each *Peromyscus* species; however, in most cases there was little consistency between the trap-station analyses and the stand-level comparisons. Multiple linear regression and logistic regression examine habitat relationships at different scales, so these results are not necessarily surprising (Block and others 1998).

Importance of Dead Wood and Effects of Forest Management on Dead Wood

The models that I developed to predict the presence of *Peromyscus* species included elements of dead wood. However, there were no consistent patterns of dead wood use at the two spatial scales (trap-station level and stand-level) I examined. Either strong patterns of use of dead wood by these species are different at different spatial scales, do not exist, or I could not detect them because of small sample sizes.

Deer mice are considered habitat generalists, so they may use elements of dead wood opportunistically. Brush mice and pinyon mice may be more specialized in their use of habitat than deer mice, but they also appear able to use a variety of habitats. When we released animals, they frequently used stumps or logs as escape cover, and I expect they also used these sites as nesting and feeding sites. However, I could not provide convincing evidence to link dead wood and *Peromyscus* species. In the Pacific Northwest, Butts and McComb (2000) and Maser and others (1981) suggested that other forms of cover (for example, fern cover) might replace logs as protective cover. This might also be the case in the Southwest, with animals using areas with shrubs or rocky substrates for hiding cover. If mice use logs as movement pathways (e.g., we observed pinyon mice running beside or on top of large [>50 cm diameter] down wood), logs may not be as readily replaced by other forms of cover.

Snags have been more studied than down wood. The importance of snags is well documented in the Southwest and in other forest ecosystems. Some species (e.g., cavity nesters) must use snags or live trees with decay; without them they lack breeding sites. Artificial devices (boxes) can be used by some species as substitutes; however, these are often costly to set up and maintain.

How might forest management affect dead wood? Live trees may be retained to use as replacement snags and logs in the future. During thinning operations, large snags and logs can be protected. Down wood can be added by piling or windrowing slash, or by felling trees. However, slash piles break down quickly and their structure changes. Slash piles may be useful as cover for only a short period of time, until the wood begins to decay and collapses and no longer provides air spaces and movement corridors (W. Block, Project Leader, Rocky Mountain Research Station, Flagstaff, Arizona, pers. comm.). The effects of prescribed fires on dead wood are less predictable. Fire can create dead wood by killing live trees, or it can remove dead wood by incinerating snags and logs. Attempts to clear debris around snags and logs to protect them during prescribed burning has had mixed success; often a large portion of the dead wood is incinerated. Continuation of these studies will help clarify the effects of forest management treatments on dead wood and habitat relationships of these *Peromyscus* species.

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Dying and Dead Hardwoods: Their Implications to Management[1]

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Abstract

Although they usually comprise less than 10 percent of forest cover in western forests, hardwoods contribute greatly to sustaining biological richness. Hardwoods are highly preferred as cavity sites, are preferred foraging sites for several bird species, encourage insectivorous mammals and amphibians, and provide preferred substrate for many cryptogams and invertebrates. In the Pacific Northwest, two cavity-nesting species choose hardwoods for 70 percent or more of their nest sites, while many prefer hardwoods, even in coastal forests where hardwoods are scarce. Because many forest-dwelling species in the Pacific Northwest show strong preferences for hardwoods, hardwoods should be retained and managed as desired trees.

Introduction

Hardwoods provide three major resources to forest-dwelling organisms: substrate, foraging sites, and suitable places to rear young (including cavity sites). They provide these resources differently than do conifers because of differences in the chemistry and structure of their leaves, bark, and wood. Though many non-vertebrates species respond positively to those differences, we concentrate on vertebrates, and note contributions to non-vertebrates only briefly. We focus on species of the Pacific Northwest, including Alaska, Alberta, British Columbia, Washington, Oregon, Idaho, Montana, and northern Nevada and California. References to other regions are included to indicate trends where forestry has been practiced longer, or where particular groups of species are well documented.

We first note differences between hardwoods and conifers that make hardwoods more favorable to some organisms. Because dying and dead hardwoods are recruited from living hardwoods, we review contributions of living hardwoods to species richness, including the role of riparian areas. We then discuss the three major contributions hardwoods make to biological richness as substrate, foraging sites, and locations to rear young. Finally, we summarize management implications of our review.

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Differences Between Conifers and Hardwoods

From the perspective of forest-dwelling organisms, hardwoods differ from conifers in their leaves, bark, and wood. Most conifer trees retain their leaves for years. In temperate regions, most broad-leaved trees and shrubs are deciduous, and invest less energy than do conifers in the production of secondary compounds to deflect herbivory (Longhurst and others 1968, Wahlenberg 1946). As a result, hardwood leaves host numerous herbivorous insects that benefit many birds (Schimpf and MacMahon 1985, Willson and Comet 1996b). As they fall to the ground, these leaves form a readily digestible litter that encourages a rich arthropod fauna, thereby benefiting ground-foraging insectivores (Hoff 1957, Willson and Comet 1996b). Because the bark of many hardwood species is relatively rich in nutrients and has a higher pH than most conifer bark (Barkman 1958), hardwoods provide preferred substrate for some epiphytic bryophytes and lichens.

The tendency for hardwood trees of the Pacific Northwest to decay earlier than conifers (Cline 1977) may be associated with bark features and is a product of differences in wood chemistry. Because hardwood bark is typically much thinner than conifer bark, small wounds can provide entry ports for fungi. Once fungi are inside, hardwoods of the Pacific Northwest are less resistant to their growth than are conifers because hardwoods produce smaller amounts of resins and toxic extractives that combat decay fungi (Anonymous 1967). Thus, hardwoods provide potential cavity sites at relatively young ages and less durable logs. Differences in wood chemistry and structure also favor particular insects. Some woodpeckers feed primarily on insects restricted to hardwoods; and where hardwoods have declined significantly, these species are threatened. The middle-spotted woodpecker *(Picoides medius),* for example, disappeared from Sweden in 1980 (Bernes 1994). In the Pacific Northwest, acorn woodpeckers *(Melanerpes formicivorus)* and some sapsucker species restrict their feeding largely to hardwoods (Beal 1911, Wells and Steeger 1999).

Hardwoods and Species Richness

Hardwood stands provide an abundant insect fauna and numerous cavity sites and have been reported as having greater vertebrate richness than conifer stands (Bruce and others 1985). Because birds are the richest vertebrate group of both insectivores and cavity users, trends in richness should be most apparent among birds. Associations of some birds with hardwoods are especially strong. In the Okanagan region of British Columbia, 94 percent of Bullock's oriole *(Icterus bullockii)* nest sites were in deciduous trees (Cannings and others 1987). In Oregon, Hagar and others (1995) reported several bird species almost exclusively associated with hardwood stands (e.g., warbling vireo *[Vireo gilvus]* and yellow warbler *[Dendroica petechia]),* including 19 species associated predominantly with trembling aspen *Populus tremuloides* (e.g., red-breasted sapsucker *[Sphyrapicus ruber]* and lazuli bunting *[Passerina amoena]).* Bunnell and others (1999) considered birds to have strong associations with hardwoods if at least two-thirds of their reported nests were in hardwood species. Under that restriction, about 40 bird species in British Columbia are strongly associated with hardwoods for nesting, and another 45 to 50 use hardwoods disproportionately to hardwood abundance.

Unmanaged stands are rarely completely conifer. *Table 1* summarizes bird data from the Pacific Northwest by stand type as determined by the most abundant tree species. Riparian was defined by proximity to water, where hardwoods are generally more abundant. In seven of the nine studies, bird species richness was highest in riparian areas or stands in which the leading species was aspen *(Populus tremuloides),* cottonwood *(Populus balsamifera),* or spruce *(Picea* spp). All of these stands were mixtures of hardwoods and conifers, occurring on moist, productive sites. The riparian area of Theberge (1976) is from gravel outwash plains, where understory was less dense than in most forested riparian areas. Because studies assessed abundance in different ways *(table 1),* we standardized measures within studies by dividing all abundance measures by the highest in a given study. Like richness, highest densities tended to occur in riparian areas or stands in which aspen, cottonwood, or spruce were common. The pattern appears to be that mixtures (such as spruce-cottonwood) increase both richness and abundance, and that moister sites (spruce and riparian) favor richness or abundance as much as the presence of hardwood tree species themselves.

Because deciduous trees and shrubs are concentrated in moister or riparian areas in the Pacific Northwest, it is difficult to separate effects of the greater productivity of these areas from the presence of hardwoods. The most consistent feature of bird communities using riparian areas is that many preferentially nest or forage in deciduous trees and shrubs (e.g., Bull and Skovlin 1982, Morgan and Wetmore 1986, Sanders and Edge 1998). Of perching birds showing significant preference for riparian areas, 70 percent (14/20) nested predominantly in hardwood trees or shrubs (Bunnell and others 1999). Deciduous vegetation supports a diverse insect fauna. As expected, all (20/20) of the perching birds that were significantly more abundant in riparian areas were primarily insectivorous during breeding, which was also true of 82 percent of the mammals, among which insectivores are less common (Bunnell and others 1999). Most forest-nesting waterfowl require cavities that commonly are more available in hardwoods than in conifers. Need for cavity sites also may explain why fisher *(Martes pennanti)* maternal dens were located in sites within or next to riparian habitat, where large, decay-prone cottonwood trees were available (e.g., Weir 1995). Mammals, reptiles, and amphibians showing positive associations to deciduous trees and shrubs, also show affinities for riparian areas where deciduous species are more abundant (Gomez and Anthony 1996, McComb and others 1993). Thus, much of the commonly higher vertebrate richness in riparian areas may be a product of the greater abundance of hardwood trees and deciduous shrubs.

To assess the role of upland hardwoods, we stratified data from 286 50-meter radius bird census plots in south central British Columbia into four classes: riparian (adjacent to water; > 85 percent conifer), hardwood riparian (> 15 percent trembling aspen), upland conifer (primarily Douglas-fir *[Pseudotsuga menzieseii]* and lodgepole pine *[Pinus contorta]),* and upland hardwood (> 15 percent trembling aspen). The richest sites were hardwood riparian sites *(fig. 1).* Upland hardwoods had significantly greater bird richness than upland conifers (least significant difference; $P = 0.04$); hardwood riparian hosted greater richness than riparian (least significant difference; $P = 0.059$). We conclude that even on upland areas, small inclusions of aspen help to increase vertebrate richness. Huff and Raley (1991) reached a similar conclusion for coastal forests.

Table 1—*Bird species richness (number of species) and abundance in stands dominated by different tree species. Highest value within a study in bold.*

	"Pure" TA[1]	TA	BCo	AL	RIP	S/H	S	S+	SF	PP	DF	LP	"Pure" LP	Source and Location
Species Richness		22.0			**24.8**		22.3				14.3	14.0	7.1	Waterhouse & Dawson 1998 - scBC
		9.5					12.1	**12.8**	**12.8**		4.0	8.3		C. Galindo-Leal & F. Bunnell[2] - seBC
		[3]15.0			14.0	14.0	**16.0**							Theberge 1976 - swYK
	24.8					**32.3**		18.7						Pojar 1995 - scBC
		24.0					22.0			**28.0**	26.0			Winternitz 1976 - CO
		23.0					16.3				13.7	8.5		K. Martin[4] - scBC
		37.0						32.0						B. Booth[5] - scBC
			20.2	19.8				17.3						Willson & Comet 1996a - seAK
		15.5	**17.0**					16.5				9.5		Willson & Comet 1996a - neBC
Standardized Abundance		0.86			**1.00**		0.99				0.54	0.51	0.23	Waterhouse & Dawson 1998 - scBC
		0.95					0.95	0.96	**1.00**		0.34	0.61		C. Galindo-Leal and F. Bunnell[2] - seBC
		[3]0.73			0.63	**1.00**	0.97							Theberge 1976 - swYK
	0.75					**1.00**		0.61						Pojar 1995 - scBC
		1.00					0.49			0.86	0.70			Winternitz 1976 - CO
		1.00					0.73				0.61	0.64		K. Martin[4] - scBC
		0.46						**1.00**						B. Booth[5] - scBC
			1.00	0.78				0.81						Willson & Comet 1996a - seAK
		0.50	**1.00**					0.56				0.22		Willson & Comet 1996a – neBC

[1] Tree species/habitat codes: TA = Trembling aspen; BCo = Black cottonwood *Populus balsamifera trichocarpa*; AL = Alder; RIP = riparian; S/H = Spruce plus hardwood (usually Balsam poplar *Populus balsamifera*); S = Spruce; S+ = Spruce plus other conifer; SF = Subalpine fir; PP = Ponderosa pine; DF = Douglas-fir; LP = Lodgepole pine.

[2] Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

[3] Balsam poplar parkland.

[4] Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

[5] Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

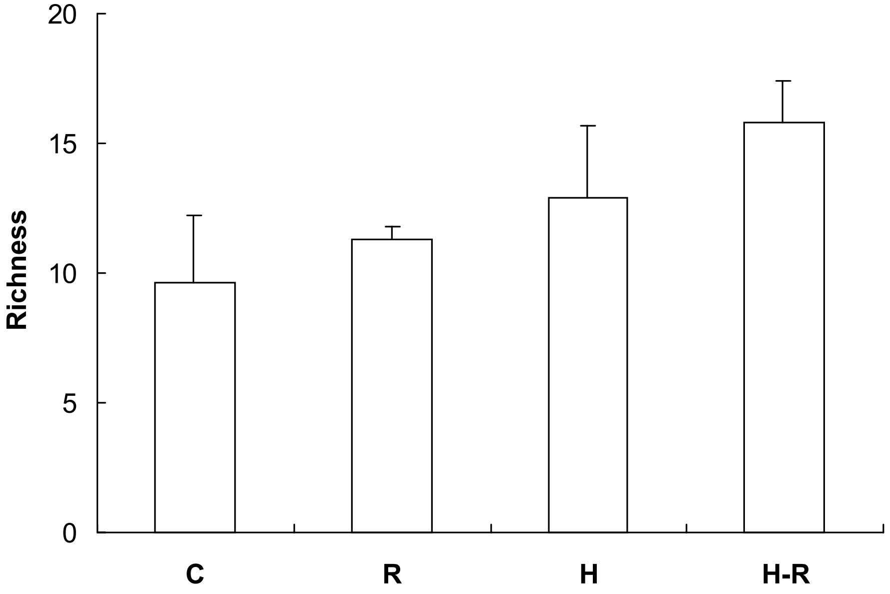

Figure 1—Mean species richness of birds in 50-m radius plots of four broad habitats: C = upland conifer, R = conifer riparian, H = upland hardwoods, HR = hardwood riparian. Numbers in parentheses are numbers of plots; error bars are standard deviation.

Hardwoods as Substrate

Hardwoods provide preferred substrate for many non-vertebrates. Aspen is particularly favored by bryophytes and lichens (Brodo 1974, Gustafsson and Ahlén 1996, Kuusinen 1994). In north and central Sweden, 20 percent of the red-listed, epiphytic bryophytes occur on aspen, despite the fact that aspen comprises only 1.5 percent of the total forest volume (Hallinbäck 1996). Berg and others (1994) reviewed 1,487 threatened species in Sweden, and found 290 restricted to old, living trees. Of those, 85 percent (mostly invertebrates) were restricted to hardwoods. Of 70 forest-dwelling mosses of the Pacific Northwest reviewed by Vitt and others (1988), at least 5 species appear restricted to hardwoods. In British Columbia, 45 lichen species are reported as largely restricted to hardwoods (Goward 1999, and Goward and others 1994). As with birds, small inclusions of hardwoods apparently encourage lichen richness within conifer stands. In montane forests of British Columbia, more lichen species occur on conifers adjacent to aspen than on conifers distant from aspen (Arsenault and Goward 2000). Among macrofungi, at least 440 species in British Columbia have hardwoods as their substrate (Fernando and others 1999). Data on invertebrate affinities for hardwoods in the Pacific Northwest are sparse, but elsewhere, aspen trunks and litter host rich invertebrate faunas (Niemelä and others 1992, Siitonen and Martikainen 1994). Small natural or experimental inclusions of aspen litter in conifer forests created aggregations of land snails and predatory forest-floor arthropods (Niemelä 1997).

Data on amounts of hardwoods required are sparse. Hazell and others (1998) evaluated responses of four aspen-specific, epiphytic bryophytes in Sweden to a range of aspen densities and found a positive response only to aspen diameter. We believe the response to diameter reflects the fact that larger trees usually have been present for a longer time. Because bryophyte dispersal distances are short (Hedenäs and others 1989; Miles and Longton 1990, 1992), dispersal must be slow. Larger trees have been available to rare colonization events for a longer period of time. Moreover, their rougher bark may provide favorable substrate for establishment. Because aspen density had little influence on epiphyte abundance but diameter did, scattered older trees may be valuable for some epiphytes. Hazell and Gustafsson (1999) evaluated survival and vitality of lichen and bryophyte transplants in mature forests, aspen patches in clearcuts (aggregated retention), and scattered trees in clearcuts (dispersed retention). Both the lichen and the bryophyte species survived on the scattered trees. Ås (1993) found that small patches of hardwoods sustained woodliving beetles. In short, many more non-vertebrate species than vertebrate species require hardwoods, and many respond positively to small hardwood inclusions within conifer forests.

Hardwoods as Foraging Sites

Insectivorous amphibians, reptiles, and mammals often show preferences for hardwood stands and associated deciduous understory, where they forage in a leaf litter rich in prey (Bunnell and others 1999). We collated studies that permitted estimation of selection by primary excavators while foraging *(table 2).* Because we were interested in direct comparisons between studies, we used Chesson's alpha (Chesson 1983). It ranges from 0.0 at complete avoidance to 1.0 when all foraging was on a single species. Of the 11 studies for which we were able to calculate alpha, hardwoods ranked first or second in preference in six. Other workers have reported foraging concentrated on hardwoods, but their data did not permit calculation of preference. For example, foraging of the red-naped sapsucker *(Sphyrapicus nuchalis)* in British Columbia was largely limited to trembling aspen and paper birch *(Betula papyrifera*; Wells and Steeger 1999), and acorn woodpeckers are almost completely restricted to hardwoods in California (Beal 1911). Although sapsuckers create sapwells in hardwoods, most woodpeckers are primarily gleaning rather than drilling when foraging on hardwoods, consistent with the rich insect fauna on hardwood trunks reported by Sittonen and Martikainen (1994). Hardwoods often provide foraging sites at smaller sizes and younger ages than do conifers (Bunnell and others 2002).

Hardwoods as Places to Rear Young

Hardwoods provide favorable sites to rear young in several ways. Many birds preferentially nest in hardwoods, and some species nesting upslope bring fledged young into hardwood riparian areas to forage on the abundant insects (Bunnell and Dupuis 1995). Insectivorous amphibians, reptiles, and mammals exploit the abundant prey in deciduous leaf litter. Still more species select hardwoods as cavity, denning, or roosting sites.

Preferential use of tree species as cavity sites usually is related to decay characteristics, but can be influenced by foraging specialization. At least 10 primary excavators in the Pacific Northwest locate most of their nests in hardwoods, and weak excavators are more likely to use hardwoods *(fig. 2).* Many studies summarized are from locations where hardwoods comprise less than 5 percent of the tree stems, yet cavity nesters often chose decay-prone hardwoods for > 80 percent of their nest sites. Studies reporting both use and availability permit estimates of selection for specific tree species. The most consistently preferred species were trembling aspen, western larch *(Larix occidentalis),* and ponderosa pine *(Pinus ponderosa*; *table 3).* Primary cavity nesters favored trembling aspen, while secondary nesters tended to favor western larch and western redcedar *(Thuja plicata).* Lodgepole pine and true firs (*Abies* sp.) were least favored as cavity nesting sites. Although black-backed and three-toed woodpeckers *(Picoides tridactylus)* often concentrate their foraging in beetle-ridden lodgepole pine (Goggans and others 1989; Machmer and Steeger),[4] they still seek aspen for nesting *(fig. 2).* Exceptions exist. Bull and others (1996) reported that all cavities used by *Vaux's* swift *(Chaetura vauxi)* were in grand fir *(Abies grandis)*. In montane forests of south central British Columbia, all 21 nests of three-toed woodpeckers were in subalpine fir *(Abies lasiocarpa;* Klenner and Huggard 1997).[5]

Comparisons between areas reveal that preference for hardwood nest trees is sometimes flexible. In the interior of British Columbia, Harestad and Keisker (1989) reported that all 243 nests of primary excavators found occurred in hardwoods, despite the fact that hardwood cover comprised only 5 percent of their study area (which was dominated by Douglas-fir). In coastal Oregon and British Columbia, the identical species nested mainly in Douglas-fir and western hemlock *(Tsuga heterophylla*; Bunnell and Allaye-Chan 1984, Mannan and others 1980). Flammulated owls *(Otus flammeolus)* exhibit similar changes over their range. Ponderosa pine and Douglas-fir were used where prevalent (Bull and others 1990, Reynolds and Linkhart 1987, van Woudenberg 1992), but elsewhere the owl nested in oaks *(Quercus* spp.) and trembling aspen (Marcot and Hill 1980, Webb 1982).

Flexibility is not universal. Although some sapsuckers select hardwoods for 80 to 95 percent of their nest sites, other woodpeckers are more emphatically restricted to conifers *(fig. 2).* Throughout its range, only 9 of 167 white-headed woodpecker *(Picoides albolarvatus)* nests have been reported from hardwoods. The restriction is a product of a diet high in ponderosa pine seeds (Dixon 1995a, Ligon 1973). Diet also may limit black-backed and three-toed woodpeckers to coniferous nest sites unless hardwood species are present in small inclusions *(appendix A).* Weaker excavators that nest and forage in conifers are potentially threatened by forest practices because the conifers may not become old and decayed enough to be susceptible to excavation. In fact, these species (black-backed, Lewis's, three-toed, and white-headed woodpecker) are listed "at risk" in one or more jurisdictions of the Pacific Northwest.

Patterns of selection of tree species reflect decay patterns. All cavity nesters appear to seek pockets of heart rot (Bunnell and Allaye-Chan 1984, Kilham 1971), but weaker excavators tend to seek trees exhibiting more advanced decay (Bunnell and others 1999). When nesting in hardwoods, bird species tend to use less visibly decayed trees than when nesting in conifers (Bunnell and others 1999). This pattern reflects both earlier onset of heart rot in hardwoods (Cline 1977, Harmon 1982), and poor applicability to hardwoods of decay classes developed for conifers. Current decay classes apply poorly to hardwoods, because hardwoods show fewer external signs of decay when decay is present. *Phellinus ignarius* can invade live aspen, softening the heartwood, while the sapwood remains unaffected and the tree shows no external sign of decay. As a result, cavity nesters are more likely to excavate living hardwoods than living conifers.

Table 2 —*Selectivity of foraging tree species by cavity nesting birds of the Pacific Northwest.*[1] *Highest value within study is in bold.*

	Tree Species												
	TA[2]	OK	PP	SP	WP	PI	DF	WF	AF	BS	ES	IC	Source
Yellow-bellied sapsucker	0.03		0.03		0.00		0.02	0.02	**0.72**	0.08	0.11		Franzreb 1983
Hairy woodpecker		**0.30**	0.21	0.10			0.08	0.21				0.10	Morrison & With 1987
		0.37	0.32	0.07			0.05	0.12				0.07	Morrison and others 1985
White-headed woodpecker		0.16	0.15	0.20			0.16	0.05				**0.29**	Morrison & With 1987
		0.21	0.22	**0.26**			0.10	0.08				0.14	Morrison and others 1985
		0.00	**0.62**			0.27						0.09	Hilkevitch 1974 (Charlton Flats)
		0.00	**0.38**			0.31		0.01				0.30	Hilkevitch 1974 (Dark Canyon)
Nutall's woodpecker		0.30				**0.70**							Block 1991
Mountain chickadee	0.05		0.02		0.03		0.08	0.10	**0.39**	0.13	0.21		Franzreb 1983
		0.19	0.12	0.12			0.15	**0.33**				0.09	Morrison and others 1985
Chestnut-backed chickadee		0.19	0.02	0.12			**0.34**	0.28				0.05	Morrison and others 1985
Red-breasted nuthatch		0.23	0.15	**0.26**			0.19	0.09				0.07	Adams & Morrison 1993
Sitta canadensis		**0.24**	0.17	0.11			0.18	0.20				0.11	Morrison and others 1985

[1] Apparent selectivity estimated by Chesson's alpha (Chesson 1983) to permit comparisons among studies.

[2] Tree species codes: TA = Trembling aspen; OK = Oak; PP = Ponderosa pine; SP = Sugar pine *Pinus lambertiana*; WP = White pine *Pinus monitcola*; PI = Pinus sp.; DF = Douglas-fir; WF = White fir *Abies concolor*; AF = Alpine fir *Abies lasiocarpa*; BS = Blue spruce *Picea pungens*; ES = Engelmann spruce *Picea engelmannii*; IC = Incense cedar *Calocedrus (Libocedrus) decurrens*.

Table 3 —*Apparent selectivity for nest tree species by cavity nesting birds of the Pacific Northwest.* [1] *Species used infrequently are not shown, but were used in calculations of selectivity. Highest selectivity within a study is shown in bold.*

	Hardwood Tree Species[3]				Coniferous Tree Species[3]												
Group[2]	TA	PB	BM	RA	DF	WL	Sx	LP	PP	WP	WRC	WH	GF	SF	WF	P[4]	Source and Comments
All	**0.98**				0.01		0.00	0.01								< 0.001	K. Martin[5]; trees & snags >12 cm dbh
All					0.22	0.09	**0.61**							0.08		< 0.001	(AZ&CO) Scott and others 1980; snags >11 cm dbh;
					0.56	0.23								0.21		0.025	(CO) PP >14 cm dbh
All								0.25							**0.35**	n/a	Raphael & White 1984; snags >13 cm dbh
All	**0.77**	0.14														< 0.001	Harestad & Keisker 1989; trees & snags >15 cm dbh
All					0.10	**0.42**		0.06	0.32				0.10			< 0.001	Bull 1980; snags >10cm dbh
P					0.00	**0.59**		0.04		0.00	0.22	0.12		0.01		< 0.001	McClelland 1977; live trees only >22 cm dbh
S					0.00	0.09		0.00		0.25	**0.65**	0.00		0.00		< 0.001	
All	**0.94**		0.02														Li & Martin 1991; trees >8 cm dbh
P	**0.81**	0.13			0.00	0.04	0.00	0.00	0.02	0.00	0.00					< 0.001	C. Steeger[6]; snags & trees > 7.5 cm dbh
S	0.00	0.09			0.00	**0.40**	0.09	0.01	0.10	0.32	0.00					< 0.001	
P				**0.77**	0.06						0.00	0.12				n/a	Avail. data from Manuwal & Zarnowitz 1981
S				0.00	0.43						**0.46**	0.00				n/a	Use data from Manuwal 1981; snags >13 cm dbh
All			0.13		0.17						0.13		**0.47**			n/a	(snags) Nelson 1988; snags & trees >10cm dbh
			0.26		0.16						**0.51**	0.02	0.05			n/a	(trees)
All			0.25								0.26	**0.49**				n/a	Allaye-Chan 1981; snags >10 cm dbh

[1] Apparent selectivity estimated by Chesson's alpha (Chesson 1983) to permit comparisons among studies.

[2] All = all cavity nesters, P = Primary cavity nesters, S = Secondary cavity nesters.

[3] Tree Species Codes: TA = Trembling aspen; PB = Paper birch; BM = Bigleaf maple *Acer macrophyllum*; RA = Red alder *Alnus rubra*; DF = Douglas-fir; WL = Western larch; Sx = White spruce *Picea glauca* and spruce hybrid; LP = Lodgepole pine; PP = Ponderosa pine; WP = Western white pine; WRC = Western red cedar; WH = Western hemlock; GF = Grand fir; SF = Subalpine fir; WF = White fir.

[4] Evaluation of significant differences in selectivity by X^2 where numbers, rather than percentages, were available.

[5] Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

[6] Unpublished data on file, Pandion Ecological Research, Ltd.; Nelson, BC, Canada.

Weak and strong excavators use live trees differently. Weak excavators show no change in the proportion of live trees selected as the proportion of hardwood nest trees changes. Most nests (78 percent) were in dead trees regardless of the tree species used (Bunnell and others 2002). Strong excavators make significantly greater use of live trees as the percentage of nest sites in hardwoods increases ($P < 0.001$ across the nine species of strong excavators included in *fig. 2,* after percentages are arcsine transformed).

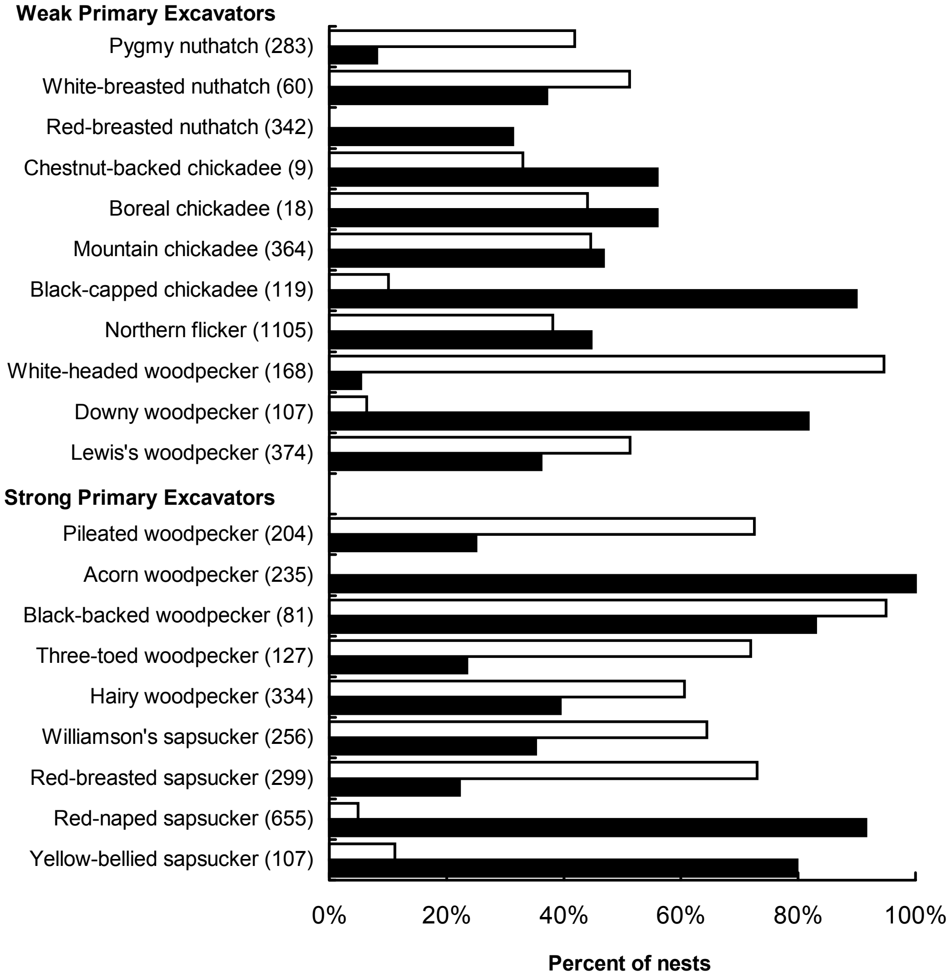

Figure 2—Percent (weighted mean) of nest sites in coniferous (☐) and hardwood (■) trees. Number of nests in parentheses.

We conclude that primary excavators select for sites easy to excavate. Generally, that means hardwoods such as aspen, cottonwood and birch *(Betula* spp.). More decay-prone hardwood species are selected over more decay-resistant species (e.g., Brush and others 1983). Where hardwood species are not common, birds excavate conifers, preferring those in which the heartwood is rotting. Smaller, weaker excavators, such as chickadees and nuthatches, sometimes seek decay-softened sapwood (Lundquist and Mariani 1991, Steeger and Hitchcock 1998). The pattern of selection of living and dead nest trees suggests that moribund hardwoods can substitute for conifer snags.

The largest denning mammals rarely find hardwoods big enough to accommodate them, but almost half of fisher den sites were in hardwoods, generally large cottonwood *(table 4).* The strong selection of hardwood roost trees, usually aspen, by some bats is not simply a product of their distribution. In at least some areas, bats actively seek out scattered hardwoods (Crampton and Barclay 1995, Vonhoff 1996). Although fewer mammal than bird species rely on hardwoods for cavity sites, hardwoods appear critical to some mammals *(table 4)*.

Table 4—Grand mean of the percent of mammal dens or roosts located in hardwood trees.

Species	Pct hardwood	n[1]	Source
Bats			
Big brown bat *Eptesicus fuscus*	14.0	24	Betts 1996; Rasheed and Holroyd 1995; Vonhof 1996
California bat *Myotis californicus*	0.0	25	Brigham and others 1997; Grindal 1997; Vonhof 1996
Little brown myotis *Myotis lucifugus*	100.0	21	Crampton and Barclay 1995; Grindal 1997; Rasheed and Holroyd 1995
Long-legged myotis *Myotis volans*	0.0	41	Ormsbee and McComb 1998; Rasheed and Holroyd 1995
Northern long-eared myotis *Myotis septentrionalis*	0.0	7	Caceres 1997
Silver-haired bat *Lasionycteris noctivagans*	100.0	50	Betts 1996; Campbell and others 1996; Crampton and Barclay 1995; Rasheed and Holroyd 1995; Vonhof 1996
Western long-eared myotis *Myotis evotis*	0.0	21	Caceres 1997; Grindal 1997; Vonhof and Barclay 1997
Big brown & silver-haired bat	4.0	24	Bull and others 1996
Big brown, silver-haired, & California myotis	64.0	31	Steeger and Machmer 1996
Rodents			
Flying squirrel *Glaucomys* spp.	33.1	650	Carey and others 1997; Mowrey and Zasada 1984; C. Steeger[2]
Red squirrel *Tamiasciurus hudsonicus*	51.5	22	K. Martin,[3] C. Steeger[2]
Red tree vole *Phenacomys longicaudus*	0.0	78	Meiselman and Doyle 1996
Carnivores			
Black bear *Ursus americanus*	0.0	16	Bull and others 1996
Fisher	45.0	35	Anonymous 1996; Weir 1995
American marten *Martes Americana*	0.0	375	Bull and Heater 1996; Jones and others 1997; Raphael and Jones 1997

[1] Number of dens and roosts.

[2] Unpublished data on file, Pandion Ecological Research, Ltd., Nelson, BC, Canada.

[3] Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

Implications to Management

A significant portion of the vertebrate fauna in western forests shows affinities with hardwoods. Bunnell and others (1999) reported that across forest types of British Columbia, 19 to 31 percent of forest-dwelling bird species located two-thirds or more of their nests in hardwoods. The degree to which trembling aspen is favored by primary cavity nesters *(table 3)* may be especially significant, because these species create cavities for other species. Although most vertebrates associated with hardwoods are birds, some amphibians, shrews, and bats are more abundant where hardwoods are more common. Because the contribution of hardwoods to vertebrate richness is vastly disproportionate to their relative abundance, it is important to maintain hardwoods in the forest.

Where forestry has been practiced longer than in the Pacific Northwest, trends are clear. A large portion of the species listed as endangered in Sweden are endangered because the original hardwood forest has been converted to conifers (Bernes 1994). Britain faces a similar situation. Holmes (1996) noted that about 400 insect species are associated with “the English oak” *(Quercus robur).* The decline of oaks and other hardwoods in Great Britain has meant that 14 bat species find both their roost sites and forage diminished (Holmes 1996). Of the 90 forest-dwelling vertebrates in the Pacific Northwest designated by state and provincial agencies as “sensitive” or “at risk,” 17 nest primarily in deciduous trees and 5 in deciduous shrubs. Other listed species, such as sharp-tailed grouse *(Tympanuchus phasianellus),* also seek hardwoods to forage.

From our review of vertebrate relations with hardwood species, we conclude that managers charged with sustaining biological richness should implement the following management practices:

- *Retain hardwoods and manage at least some as desired trees, rather than as competition with crop trees*—Small amounts of hardwoods intermixed with conifers serve to increase the richness of birds, bryophytes, and lichens, but there is no apparent need to retain deciduous trees in every stand. Vegetation management in young stands should not remove all hardwood stems. Instead, brushing should be of variable intensity through a block, or focused on those trees directly interfering with coniferous crop trees. A component of hardwood stems should be retained intentionally and managed to become mature trees. Hardwood snags are less durable than conifer snags and cannot substitute completely for conifers.

- *Avoid conversion of riparian areas to conifers*—Hardwoods often do better in riparian areas and little effort is required to promote them there. Hardwoods provide a number of values, including cavity sites younger than conifers, and tend to be more wind-firm than are conifers.

- *Encourage upland patches of hardwoods in areas where sustaining biodiversity is a priority*—Several vertebrates are closely associated with hardwoods, particularly aspen, willow *(Salix* spp.), or cottonwood in riparian areas. Other vertebrate species appear to benefit, but are more flexible in their requirements. Inclusions of > 15 percent aspen stems in upland areas significantly increases bird richness *(fig. 1),* and small patches sustain a variety of other organisms (Ås 1993; Hazell and Gustafsson 1999). Where patches are retained, adjacent areas should not be subject to intensive vegetation management.

- *Control domestic grazing in riparian areas*—In many western regions, hardwoods are concentrated in riparian areas. In riparian areas subject to grazing, declining amounts of hardwoods have affected abundance and distribution of vertebrates (Krueper 1992, Skovline 1984).

Endnotes

[4] Unpublished data on file, Pandion Ecological Research, Ltd.; Nelson, BC, Canada.

[5] Unpublished data on file, BC Ministry of Forests, Kamloops, BC, Canada.

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Appendix A—*Tree species used as nest sites by primary cavity nesters in the Pacific Northwest. Unidentified trees, poles, and stumps are not included.*

	Number of nest trees	Percent use of hardwoods[1]	Sources[2]
Strong Excavators			
Yellow-bellied sapsucker *Sphyrapicus varius*	97	79.8 (73-100)	5, 11
Red-naped sapsucker	715	91.5 (83-100)[3]	5, 7, 8, 18, 19, 20, 26, 27
Red-breasted sapsucker	284	22.2 (1-65)	5, 9, 16, 19, 25
Williamson's sapsucker *Sphyrapicus thyroideus*	268	35.2 (0-97)	4, 5, 7, 8, 19, 25
Hairy woodpecker *Picoides villosus*	346	39.4 (0-100)	4, 5, 7, 9, 18, 19, 20, 25, 27
Three-toed woodpecker	127	23.5 (0-75)	5, 7, 14, 17, 20, 27, 28
Black-backed woodpecker *Picoides arcticus*	81	0.8 (0-4)	4, 5, 13, 25, 27
Acorn woodpecker	235	100.0 (100-100)	15, 19
Pileated woodpecker *Dryocopus pileatus*	199	25.0 (0-100)	1, 3, 5, 18, 20, 22, 27
Weak Excavators			
Lewis's woodpecker *Melanerpes lewis*	488	36.1 (0-74)	2, 5, 7, 12, 25
Downy woodpecker *Picoides pubescens*	102	81.7 (50-100)	5, 7, 19, 20, 27
White-headed woodpecker	173	5.4 (0-7)	5, 7, 10, 23, 25, 29
Northern flicker *Colaptes auratus*	998	44.7 (0-97)	4, 5, 7, 9, 18, 19, 20, 25, 27
Black-capped chickadee *Poecile atricapillus*	27	89.9 (88-100)	5, 7, 20, 27
Mountain chickadee *Poecile gambeli*	332	46.8 (3-98)	5, 17, 19, 20, 25
Boreal chickadee *Poecile hudsonicus*	18	56.0 (56-56)	24
Chestnut-backed chickadee *Poecile rufescens*	8	56.0 (56-56)	27
Red-breasted nuthatch *Sphyrapicus ruber*	238	31.3 (0-89)	6, 18, 20, 25, 27
White-breasted nuthatch *Sitta carolinensis*	56	37.1 (0-100)	6, 19, 21, 25
Pygmy nuthatch *Sitta pygmaea*	300	8.1 (0-89)	6, 7, 19, 21, 25

[1] Weighted mean for all studies. Range among individual studies in parentheses.

[2] 1 = K. Aubry and C. Raley (unpublished) in Bull and Jackson 1995, 2 = Bock 1970, 3 = Bull 1987, 4 = Bull and others 1986, 5 = Campbell and others 1990, 6 = Campbell and others 1997, 7 = Cannings and others 1987, 8 = Crockett and Hadow 1975, 9 = Deal and Gilmore 1998, 10 = Dixon (1995b), 11 = Erskine and McLaren 1972, 12 = Galen 1989, 13 = Goggans and others (1989), 14 = Hågvar and others 1990, 15 = Hooge and others 1999, 16 = Kelleher 1963, 17 = Klenner and Huggard 1997, 18 = Klenner, W. and D. Huggard, 19 = Li and Martin 1991, 20 = Martin, K., 21 = McEllin 1979, 22 = Mellen 1987, 23 = Milne and Hejl 1989, 24 = Peck and James 1987, 25 = Raphael and White 1984, 26 = Steeger and others 1996, 27 = Steeger, C., 28 = Wesolowski and Tomialojc 1986, 29 = Western Foundation of Vertebrate Zoology (no date) in Garrett and others 1996.

[3] Where Cannings and others 1987 and Campbell and others 1990 or 1997 occur together, Cannings and others 1987 is not included in the weighted mean.

Diameters and Heights of Trees with Cavities: Their Implications to Management[1]

Fred L. Bunnell,[2] Elke Wind,[3] Mark Boyland,[4] and Isabelle Houde[4]

Abstract

Primary cavity nesters select larger trees when nesting in conifers than when nesting in hardwoods. Larger birds use larger nest trees, but the trend is more weakly expressed in hardwoods, as is expected if rot governs nest tree selection. Birds select larger nest trees in more productive coastal forests than in inland forests. Actual nest heights are much shorter than nest tree heights, but species-specific averages are rarely below 5 meters. Larger mammals require older, larger trees where rot is advanced. Bats also use larger trees, particularly when roosting in conifers. Sustaining all cavity users requires sustained provision of a range of diameters of decaying and dead trees, including some trees at least 50 cm dbh (smaller in less productive forests).

Introduction

Dying and dead trees are common in unmanaged forests, and cavity users typically represent 25 to 30 percent of the terrestrial vertebrate fauna in forests of the Pacific Northwest (Bunnell and others 1999, Thomas and others 1979). Proportions are less where trees are smaller, as in the spruce-willow-birch zone of British Columbia (Bunnell and others 1999). Forest practices reduce cavity sites by reducing amounts of moribund and dead wood and by reducing the size of trees compared to that formerly present. As a result, lack of cavity sites is the most frequently reported threat to forest-dwelling species, including 28 taxa designated "at risk" in the Pacific Northwest (Bunnell and others 1999).

The only compelling way of selecting goals for what we should retain or produce as nest and den trees is to evaluate patterns that the animals exhibit in their selection. We first review cavity-using species and broad factors governing snag use. We then examine patterns of selection among available trees and as a function of the size of bird. From these patterns we derive management implications. We treat both birds and mammals, but focus on primary excavators of the Pacific Northwest,

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including Alaska, Alberta, British Columbia, Washington, Oregon, Idaho, Montana, and northern Nevada and California.

Species Using Cavities

In the Pacific Northwest, 69 vertebrate species consistently use cavities and more species make opportunistic use (Bunnell and others 2002). Birds (48 species) and bats (13 species) represent 88 percent of the species consistently using cavities. More bird than mammal species use cavities, but the proportion of mammalian users is higher, ranging in size from long-legged myotis *(Myotis volans)* to black bears *(Ursus americanus)* (Bunnell and Chan-McLeod 1997, Cannings and Harcombe 1990, Peterson and others 1993, Whitaker 1993). Other than some bats and squirrels, mammal use of cavities is more opportunistic than it is for birds. Amphibians and reptiles also use snags and stumps opportunistically (Bunnell and Dupuis 1995, Stelmock and Harestad 1979).

Cavity users can be divided into three groups: species that excavate their own cavities (primary cavity nesters such as woodpeckers); species that use holes excavated by primary cavity nesters (secondary cavity users such as buffleheads *[Bucephala albeola]*[5] and flying squirrels [*Glaucomys* sp.]); and species that use other types of cavities (e.g., Vaux's swifts *[Chaetura vauxi]* and black bears) (Bunnell and others 2002). Most woodpeckers are strong primary cavity nesters, especially adapted for excavating (Spring 1965), and forage primarily by drilling in trees or snags. Weak primary cavity nesters, such as chickadees and nuthatches, are less well adapted for excavation and sometimes modify existing cavities rather than make their own (McClelland and others 1979). Strong excavators are generally large birds, while weak excavators are mainly smaller species. Exceptions to these generalizations include some larger species that are relatively weak excavators (e.g., Lewis's woodpecker *[Melanerpes lewis]*, white-headed woodpecker *[Picoides albolarvatus],* and northern flicker *[Colaptes auratus]).*

If habitat requirements of the primary excavators are not met, secondary cavity users also may be lost (Daily and others 1993, Dobkin and others 1995). Larger woodpeckers and the northern flicker thus play a key role in forest ecosystems, providing nest holes for other cavity-nesting birds and roosts or dens for other birds and mammals (Bull and others 1986). Similarly, the sapwells of sapsucker create feeding opportunities for at least 23 bird species, 6 mammal species, and 9 Orders and 22 Families of arthropods (Foster and Tate 1996, Miller and Nero 1983, Sutherland and others 1982). Moreover, woodpeckers can constrain abundance of forest "pest" insects (Holmes 1990, and Thomas and others 1979). Because of these contributions, strong excavators have been termed "keystone species" (e.g., Dailey and others 1993), whose loss would substantially alter forest ecosystems. In the Pacific Northwest, only 10 of the 69 cavity-using species present are strong enough excavators to create habitat for other vertebrates. We emphasize primary cavity nesters because of the role they play in supporting other species.

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[5] Unpublished data on file, Center for Applied Conservation Research, University of British Columbia, Vancouver, BC, Canada.

A General Model of Cavity Use

Cavity-nesting birds benefit from the protection from predators that cavities provide their young, as well as shelter and insulation of the nest or roost (Miller and Miller 1980, O'Connor 1978). Size of cavity may affect productivity. Eriksson (1979) reported greater productivity of common goldeneyes *(Bucephala clangula)* in larger nest boxes. The cost for primary cavity-nesters is the time and energy required to excavate the cavity: about 20 days for hairy woodpeckers *(Picoides villosus)* (Ehrlich and others 1988). Ideally, a cavity nest is located where the outer wood is hard, to prevent predators from tearing open the nest, but the inner wood is soft, to allow easy excavation. Soft inner wood is preferred due to the mechanics of chiseling wood in an enclosed space. Heart rots, whether extensive or local, are of prime importance. Generally, all primary excavators seek decayed heartwood, although the strongest excavators do not require it (Bunnell and Allaye-Chan 1984, Kilham 1971, Shigo and Kilham 1968). For weak primary cavity-nesters, harder outer wood remains desirable to reduce predation, but these species cannot excavate hard wood. They must either compromise with softened sapwood, or find existing holes in hard outer wood, such as those created at dead branch stubs.

The ideal cavity nest also should be high in a tree to avoid terrestrial nest predators. The bole where the nest is located must be wide enough to allow a cavity large enough to contain nestlings. These factors promote preference for large-diameter trees, in which the stem is a suitable width well above the ground. The importance of softened heartwood also promotes preference for larger stems, because large stems are usually older stems that have developed heart rot. These needs for soft or hardwood, appropriate stem diameter at the nest, and height above the ground explain many of the preferences researchers have observed among cavity nesters. Most recommendations for snag management derive from these same considerations.

Unlike primary cavity-nesters, secondary cavity-users "take what they can get," with certain limitations. The most obvious limitation is that nest holes must be big enough. Mountain bluebirds *[Sialia currucoides]*, for example, rely primarily on nests made by flickers rather than those of smaller woodpeckers or sapsuckers (Dobkin and others 1995). The nest also needs to be near appropriate habitat, which is not the forest for many secondary users (e.g., cavity-nesting ducks, swallows, bluebirds, and American kestrels *[Falco sparverius]).* Because secondary users are relatively abundant compared to primary excavators, competition for cavities is often intense (Bock and others 1992, von Haartman 1957). Some secondary users, however, show strong preferences among cavity sites. For example, because of their high energy demands and temperature sensitivity, bats often select cavities with favorable microclimates *(*Kalcounis and Brigham 1998, Lewis 1995).

In the Pacific Northwest there are 23 primary cavity nesters and 40 secondary cavity users. Another six species use dying and dead trees differently. Some cavity users (raccoons *[Procyon lotor]*, American martens *[Martes Americana]*, fishers *[Martes pennanti]*, black bears) are too large to use cavities excavated by woodpeckers. They must rely on large cavities formed by decay or fire. These cavities are uncommon, because old, large trees are uncommon. Vaux's swifts nest and roost in hollow snags large enough that they can fly up and down the hollow chamber (Baldwin and Zaczkowski 1963). Brown creepers *[Certhia Americana]* nest under slabs of loose bark on snags and old trees (Davis 1978). Some bats do as well, but also use cavities. Requirements of these six species can be considered individually during management.

Diameters

Larger diameter trees or snags are clearly preferred by cavity-nesting birds *(tables 1, 2)*. Nest tree diameters must be large enough to accommodate a cavity with room for an adult bird and nestlings, but sizes usually exceed that requirement. The selection of trees larger than the size of cavity required likely reflects age and the size at which heart rot develops. Flammulated owls *[Otus flammeolus]*, for example, are only slightly larger than a sparrow, but nested in ponderosa pine *[Pinus ponderosa],* averaging 57.7 centimeters in diameter at breast height (dbh) on southern aspects and 71.7 centimeters on northern aspects (data of van Woudenberg 1992). The difference reflects greater rates of growth on north aspects, and thus size at the age when rot appears.

Table 1—*Selection of nest tree diameter within different tree species by cavity-nesting birds of the Pacific Northwest (assessed by relative diameter).[1] Highest value in bold.*

Tree species[2]	**P[3]**	**S**	**All**	**P**	**S**	**P**	**S**
TA	1.15	1.38				2.15	2.11
PB						1.57	2.29
BCo							
DF	3.32	3.93					
SPR	1.03		1.29	1.32	1.32		2.81
WRC				2.36		1.97	1.40
PP			1.08			2.59	2.18
LP		1.81	1.38			1.34	1.59
WL				1.36	1.49	2.22	1.61
WP					1.94		
SF			1.57	1.08			
WH				0.81			
GF							
Source and Comments	K. Martin[4]	(trees & snags > 12 cm dbh)	Scott and others 1980 (snags > 11 cm dbh; PP > 14 cm)	McClelland 1977	(trees > 22 cm dbh)	C. Steeger[5]	(trees > 7 cm dbh)

[1] Relative diameter = mean diameter used/mean diameter available.

[2] Tree Species Codes: TA = Trembling aspen; PB = Paper birch *(Betula papyrifera);* BCo = Black cottonwood (*Populus balsamifera* ssp. *Trichocarpa)*; DF = Douglas-fir; SPR = Spruce *(Picea)* spp.; WRC = Western redcedar *(Thuja plicata)*; PP = Ponderosa pine; LP = Lodgepole pine (*Pinus contorta)*; WL = Western larch *(Larix occidentalis);* WP = White pine *(Pinus monitcola);* SF = Subalpine fir; WH = Western hemlock *(Tsuga heterophylla);* GF =Grand fir. (Sources of tree names are Crittenden 1992, Pojar and MacKinnon 1994, and Parish and others 1996.)

[3] All = all cavity nesters, P = Primary cavity nesters, S = Secondary cavity nesters.

[4] Unpublished data of K. Martin, Center for Applied Conservation Research, Faculty of Forestry, University of British Columbia, Vancouver, BC.

[5] Unpublished data of C. Steeger; Nelson, British Columbia.

Table 2—*Selection of nest tree diameter by diameter class in old-growth and second-growth stands. Selection is measured by Chesson's alpha (Chesson 1983).*

	Diameter class (cm)							
	Second-growth			**Old-growth**				**Source and Notes**
	10-19	20-49	>50	10-19	20-49	>50		Lundquist and Mariani 1991
P	0.00	0.10	0.90	0.00	0.23	0.77		(snags & trees)
	10-19	20-49		50-99	>99			
All	0.01	0.09		0.25	0.66			Nelson 1988 (snags)
	15-23	23-38	28-53	>53				Madsen 1985
All	0.03	0.09	0.15	0.73				(snags)
	15-19	20-24	25-29	30-34	35-39	>40		Harestad and Keisker 1989
P	0.02	0.07	0.18	0.23	0.22	0.27		(trees)
	15-27	28-52		53-77	78-102	103-127	>128	Schreiber and deCalesta 1992
All	0.05	0.20		0.17	0.22	0.19	0.16	(snags)

We collated data from Pacific Northwest forests relating nest tree diameter to size of bird when nesting in either hardwoods or coniferous trees, and found 162 estimates for 19 bird species *(fig. 1)*. The same bird species selected smaller trees when nesting in hardwoods than when nesting in conifers *(fig. 1)*.

For example, mean dbh of nest trees of pileated woodpeckers *(Dryocopus pileatus)* nesting in ponderosa pine was 84 centimeters, but only 40.0 and 46.6 centimeters when nesting in trembling aspen *(Populus tremuloides)*. When nesting in hardwoods or inland conifers, there is a significant trend for larger birds to use larger trees but not in coastal conifers. The latter observation suggests that coastal conifers attain large sizes before even small pockets of rot develop. The same bird species selected larger conifers in coastal forests than in inland forests *(fig. 1b)*. Hardwood data were combined because we had only seven coastal samples. The trend to select larger trees with increasing bird length is more weakly expressed in hardwoods. Each finding is expected if rot governs selection of nest trees. In the Pacific Northwest, hardwoods generally rot at younger ages and smaller sizes than do conifers (Bunnell and others 1999, Cline 1977). Because there is little relationship between degree of decay and size of hardwood trees, larger primary excavators need not consistently seek larger hardwoods. More time is required for heart rot to develop in conifers, and trees are larger before sizeable decay pockets accrue. Thus, larger bird species seeking larger pockets of heart rot seek older and larger conifers.

Milling efficiency constrains the sizes of trees grown in managed forests. Optimal milling efficiency varies with mill configuration, but for many sawmills in the Pacific Northwest the preferred maximum log diameter is < 46 to 50 centimeters (Bunnell and others 1997). Primary cavity nesters for which mean diameters of conifer trees consistently exceeded 50 centimeters dbh in inland forests include red-breasted, yellow-bellied and Williamson's sapsuckers *[Sphyrapicus thyroideus]*, white-headed and pileated woodpeckers, and the northern flicker *(fig. 1)*. Three of these 6 species are designated "at risk" in the Pacific Northwest. In coastal forests, some small birds (chestnut backed chickadee *[Poecile rufescens]*, red-breasted nuthatch *[Sitta canadensis])* consistently selected nest trees with a mean dbh > 50 centimeters, indicating the dominant role of decay in nest site selection. For inland forests, McClelland (1977) suggested that trees must be at least 23 centimeters dbh before providing a nesting site. Smaller mean values have been reported for black-capped and mountain chickadees *[Poecile gambeli]*, red-breasted nuthatches, and downy woodpeckers *[Picoides pubescens]*, especially when nesting in hardwoods *(fig. 1)*.

Shape of the diameter distribution is more important than the mean. Cumulative frequency distributions of diameters and heights of both "active" snags (used by birds for nesting) and "inactive" or unused snags tend to have a long tail of larger snags, although active snags are more normally distributed *(fig. 2)*. Using non-parametric tests, Bunnell and Allaye-Chan (1984) found that active snags were larger (height and diameter) than inactive snags in old-growth areas ($P < 0.05$); and that second-growth snags were smaller than either active or inactive old-growth snags ($P < 0.01$). Only 10 to 17 percent of nest sites were located in snags < 46 centimeters dbh *(fig. 2a)*. *Figure 2b* illustrates the cumulative frequency distribution of diameters of all aspen nest trees on 21 sites (a range of about 15 to 75 centimeters dbh).[4] Somewhat more than 50 percent of the nests were in trees < 30 centimeters dbh, and the central tendency was located around 30 centimeters dbh. Of 17 cavity nesting species nesting in aspen, four had mean nest tree diameters > 30 centimeters dbh (northern flicker, pileated woodpecker, American kestrel, and European starling *[Sturnus vulgaris])*.[4] The long tail of the distribution to the right elevates calculated mean diameters for most species *(fig. 2)*. That pattern also is evident in data of Steeger and Machmer[6] *(fig. 2c)*. Most data on snag use are collected from unmanaged forests. *Figure 2d* compares nest trees selected by red-breasted nuthatches in managed and unmanaged forests of different tree species. The similarity of snag sizes selected suggests some governing relationship within the two disparate forest types.

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[6] Unpublished data on file, Pandion Ecological Research Ltd., Nelson, British Columbia, Canada.

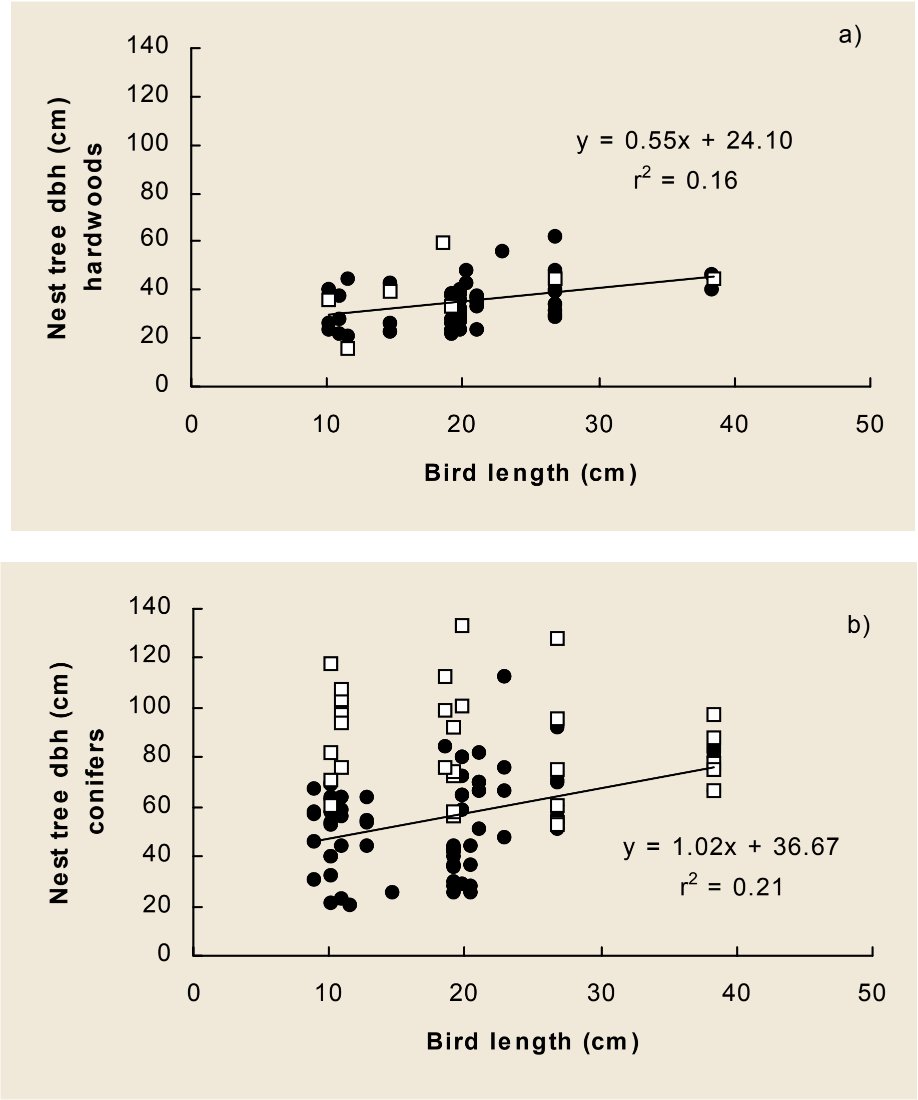

Figure 1—Mean dbh of primary excavator nest trees or snags as a function of bird length (bill to tail length) in inland (●) and coastal (☐) forests of the Pacific Northwest: a) nesting in hardwoods; b) nesting in conifer trees. All lengths from DeGraaf and others 1991. Other sources: B. Booth (unpublished); Bull 1987; Bull and others 1986; Bull and others 1992; Conway and Martin 1993; Cunningham and others 1980; Galen 1989; Harris 1982; Keisker 1987; Linder 1994; McClelland and others 1979; Peterson and Gauthier 1985; Putnam 1983; Schreiber and deCalesta 1992; Tashiro-Veirling 1994; Zarnowitz and Manuwal 1985; plus the following that are common with *figure 3:* K. Aubry and R. Raley (unpublished) from Bull 1980; Bull and Jackson 1995; Crockett and Hadow 1975; Dixon 1995a; Dixon 1995b; Dobkin and others 1995; Goggans and others 1989; Kelleher 1963; W. Klenner and D. Huggard (unpublished); Li and Martin 1991; Lundquist and Mariani 1991; M. Machmer and C. Steeger (unpublished); Madsen 1985; Mannan 1982; Mannan and others 1980; K. Martin (unpublished); McClelland 1977; McEllin 1979; Mellen 1987; Milne and Hejl 1989; Nelson 1988; Raphael and White 1984; Scott and others 1980; Sedgwick and Knopf 1990; Steeger and Hitchcock 1998; Steeger and others 1996.

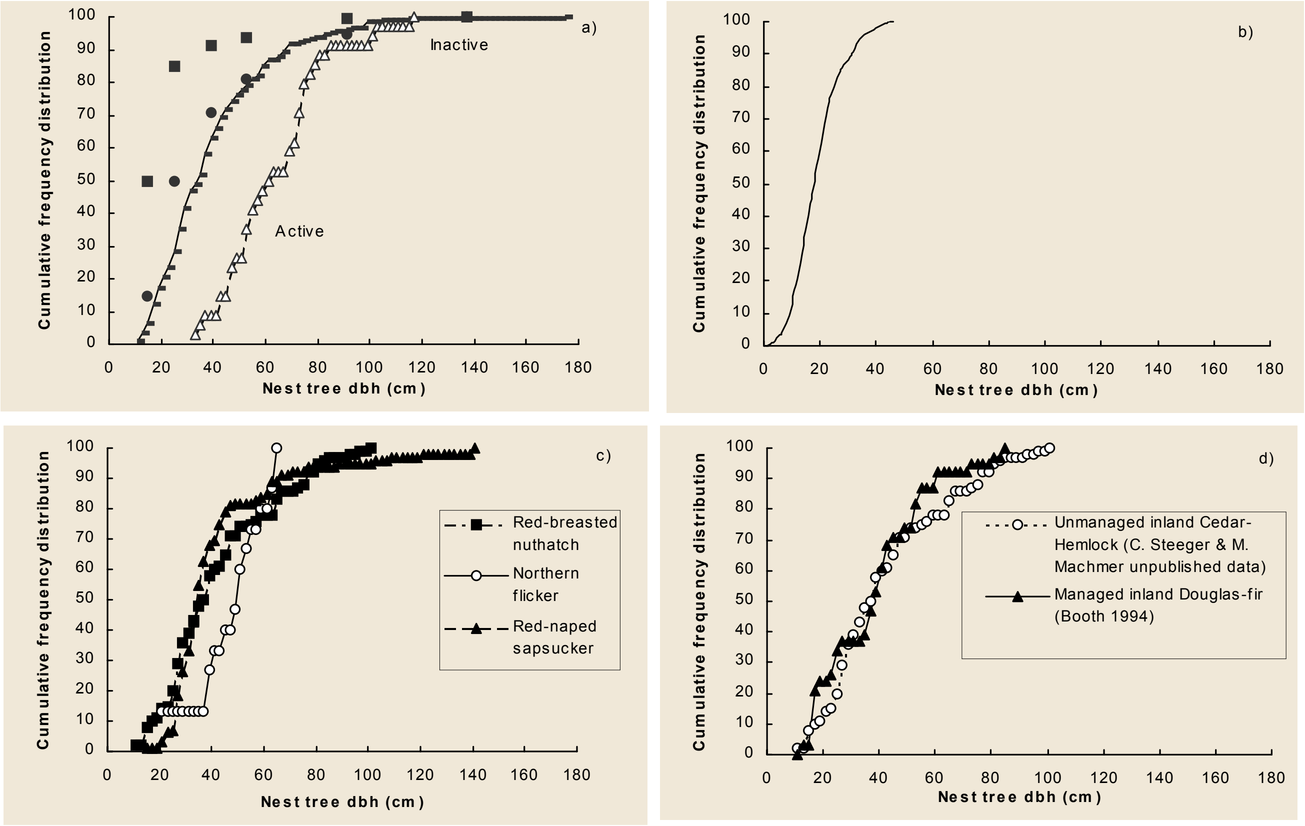

Figure 2—Cumulative frequency distributions (percent) of snag and nest tree measurements: a) dbh of old growth snags without cavities (inactive), old growth snags with cavities (active), and snags in younger stands, 70 (■) and 100 (●) years of age (all inactive; data of Cline 1977:33 and Bunnell and Allaye-Chan 1984:361-362 for the Coastal Western Hemlock zone); b) dbh of aspen nest trees in the Cariboo (data of K. Martin); c) dbh of nest trees used by three species in unmanaged Interior Cedar-Hemlock (data of C. Steeger and M. Machmer for the Interior Cedar-Hemlock zone); d) dbh of nest trees used by red-breasted nuthatches.

We derive three points from *(fig. 2)*. First, birds show a central tendency in nest tree selection, even across different forest types (see also Connor 1976, Connor and others 1975). Second, because of the long tails to distributions, this tendency is better reflected by medians (which typically are smaller than means). Unfortunately, means are more often reported. Third, minimum nest tree diameter is a poor management target, because it ignores the central tendency.[4] A more appropriate management target would be to provide trees larger than the median diameter at which heart rot commonly accrues in that forest type.

Roost trees, as well as nest trees, tend to be large. Unlike nests, which often are excavated anew each year, roosts usually are sought in natural cavities. Bull and others (1992) reported that the average diameter of 123 pileated woodpecker roost trees was 71 centimeters. Most of these were grand fir *(Abies grandis)* extensively decayed by Indian paint fungus *(Echinodotium tinctorium).* Pygmy nuthatches *(Sitta pygmaea)* use communal roosts housing up to 100 birds during winter (Sydeman and Guntert 1983). In Arizona, these roost sites averaged 73.2 centimeters dbh (Hay and Guntert 1983). Similarly, the hollow trees or snags used by Vaux's swift must be large enough to allow the swift to fly up and down. Bull and Collins (1993) reported the mean dbh of 50 nest trees of Vaux's swift to be 68 centimeters.

Mammals also select large trees for cavity sites *(table 3).* In some instances, the trees are uncommonly large. Along the coast, from Vancouver Island south through Oregon, most black bear's dens are in large dead or dying trees and downed wood (Bunnell and others 1997, Davis 1996). In drier, inland forests where soil moisture favors earth dens, Bull and others (1996) reported that 41 percent (24/59) of black bear dens were in wooden structures.[5] Mean dbh of hollow, black bear den trees is > 100 centimeters in both coastal (Davis 1996) and inland forests (Bull and others 1996). Bats also use larger trees *(table 3)* because they often use either natural hollows or cavities excavated by woodpeckers. The difference between hardwoods and conifers persists. Diameters of bat roost trees in southeastern British Columbia, averaged 52.5 centimeters dbh in Douglas-fir *(Pseudotsuga menzieseii),* but only 42.1 centimeters in trembling aspen (Steeger and Machmer 1996). Four species in *table 3* that use trees or snags > 50 centimeters dbh contain taxa listed as "sensitive" or "at risk" in the Pacific Northwest (northern long-eared myotis *[Myotis septentrionalis]*, black bear, fisher, and American marten).

Most cavity-using birds and mammals of the Pacific Northwest seek large trees as cavity sites. Eight species "at risk" use trees or snags averaging > 50 centimeters dbh, which is greater than optimal milling diameter of most sawmills. Intensive fiber production is incompatible with sustaining habitat for these species.

Heights

The fact that dbh of trees used for nesting may be much larger than the size of cavity sought by birds reflects the benefits of nesting high in trees to afford greater protection from mammalian predators (Nilsson 1984). Mean nest heights of all species but black-capped chickadee *(Poecile atricapillus)* are well above 5 meters *(fig. 3b).* In *tables 4-5* we collate data on nest heights by tree species and compare them to availability. The average height of nest trees is not consistently higher than the average height of trees in the stand *(table 4),* because many nests were in snags with broken tops. For example, in interior Douglas-fir of British Columbia, 14 of 20 nests of red-breasted nuthatches were within 2 meters of the top of decay class 4 Douglas-fir snags with broken tops (Thomas and others 1979); 21 of 22 nests in Englemann spruce-subalpine fir forest were in similar class 4 subalpine fir *(Abies lasiocarpa)* snags, broken off by wind and heart rot.[7] Small, weak excavators seek soft substrate, commonly found in short, broken-topped snags or stumps. That tendency is more apparent among chickadees than nuthatches, and accounts for some of the short nest tree heights in *figure 3a.* Some mid-sized, weak excavators, also seek out well-rotted substrates in older, broken-topped snags or stumps (e.g., downy, black-backed, three-toed, and Lewis's woodpeckers; *fig. 3b).*

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[7] Unpublished data on file, British Columbia Ministry of Forests, Kamloops, British Columbia, Canada.

Table 3—*Dimensions of trees and snags used as denning and roosting sites by mammals, weighted means by species.*

	Trees			Snags			Trees & Snags Pooled			
Species	dbh (cm)	height (m)	n	dbh (cm)	height (m)	n	dbh (cm)	height (m)	n	Source
BATS										
Big brown bat *Eptesicus fuscus*	44.6	24.6	13	54.8	25.8	8	76.3		4	Betts 1996, Rasheed & Holroyd 1995, Vonhof 1996
California myotis *Myotis californicus*	34.0		2	55.5	26.6	23				Brigham and others 1997, Grindal 1997, Vonhof 1996
Little brown myotis *Myotis lucifugus*	68.5	21.4	16	40.3	11.2	3	41.4			Crampton & Barclay 1995, Grindal 1997, Rasheed & Holroyd 1995
Long-legged myotis		40.0	4	95.5	37.5	37	100.0		4	Ormsbee & McComb 1998, Rasheed & Holroyd 1995
Northern long-eared myotis	102.2	35.5	4	67.7	30.5	3				Caceres 1997
Silver-haired bat *Lasionycteris noctivagans*	37.1	24.3	18	39.0	15.5	8	45.1		25	Betts 1996, Campbell and others 1996, Crampton & Barclay 1995, Rasheed & Holroyd 1995, Vonhof
Western long-eared myotis *Myotis evotis*	72.7	49.0	2							Caceres 1997
Big brown and Silver-haired bat							68.0	22.0	6	Bull and others 1996
Big brown, Silver haired, California myotis							46.0	24.0	31	Steeger & Machmer 1996
RODENTS										
Flying squirrel	62.7	33.3	445	61.0	13.9	190	31.5		66	Carey and others 1997[1], Mowrey & Zasada 1984, C. Steeger[2]
Red squirrel *Tamiasciurus hudsonicus*		18.3	10				33.2		24	K. Martin[3], C. Steeger[2]
Red tree vole *Phenacomys longicaudus*	99.4	24.3	78							Meiselman & Doyle 1996[1]
CARNIVORES										
Black bear	161.8		5	114.0	19.0	16	152.1		43	Akenson 1994, Bull and others 1996, Davis 1996, Lindzey & Meslow 1976, Noble and others 1990
Fisher	71.3		28							Anon. 1996, Weir 1995
American marten	84.0		218	84.1	10.6	152	78.9	23.0	36	Martin & Barrett 1991, Raphael & Jones 1997, Spencer 1987

[1] Includes old-growth and second-growth/mature/young sites.

[2] Unpublished data on file, Pandion Ecological Research Ltd., Nelson, BC, Canada.

[3] Unpublished data on file, Centre for Applied Conservation Biology, University of British Columbia, Vancouver, BC, Canada.

Although larger birds use taller trees and snags ($P < 0.001$), there is great variability due to broken tops *(fig. 3a).* The same species tended to use taller trees in coastal forests than in the less productive inland forests, and the slope of the relationship is greater ($P < 0.01$). Actual nest height shows no relation with size of the bird *(fig. 3b;* $r^2 < 0.05$). The lack of relationship between bird size and nest height is expected, because the stem taper means that their larger cavities cannot be as near the top of the tree as those of smaller birds. Taller trees often are selected by cavity-nesting birds, but primarily because birds are seeking a large diameter tree with a nest site well above the ground. Management targets can be based on diameters alone.

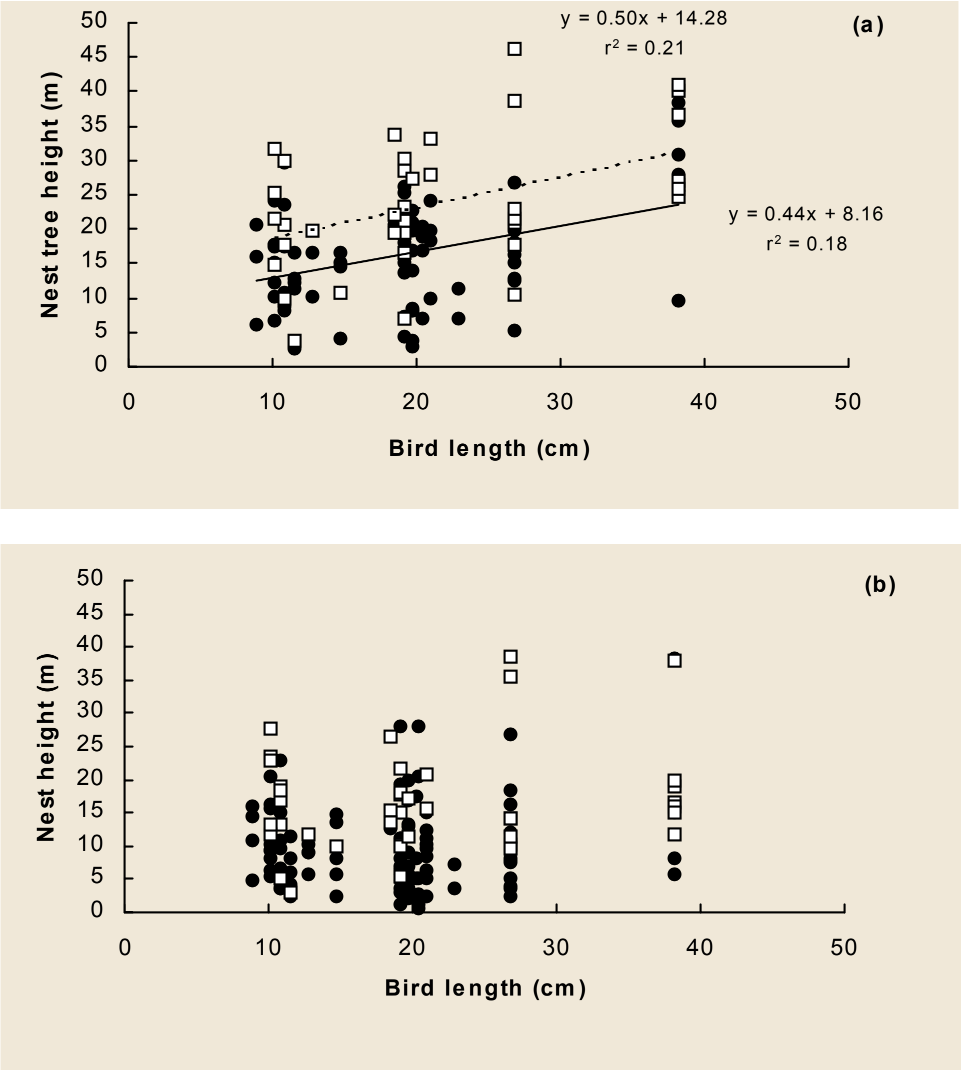

Figure 3—Mean height of primary excavator nest trees or snags (a) and nests (b) as a function of bird length (bill to tail) in inland (●) and coastal (□) forests of the Pacific Northwest. All lengths from DeGraaf and others 1991. Other sources: Franzreb 1975, Hooge and others 1999, Mannan 1977, Manuwal 1981, Medin 1985, Miller and Bock 1972, Troetschler 1976, Western Foundation of Vertebrate Zoology in Garrett and others 1996, plus those common with *figure 1.*

Table 4—*Selection of nest tree heights within different tree species by cavity nesting birds of the Pacific Northwest (assessed by relative height).*[1]

	Group[2]			
Tree species[3]	**P**	**S**	**P**	**S**
TA	RH	RH	RH	RH
PB	n/a[4]		1.90	1.79
BCo	n/a	0.89	1.09	1.25
DF	n/a		0.99	0.56
SPR	0.48	0.78		1.41
WL	0.72		1.35	1.42
WRC	0.77		1.54	1.41
PP	1.36		0.90	n/a
SF	n/a			1.10
WH	0.31		1.29	
LP	0.68			
GF				
Source and Notes	McClelland 1977	(Avail. = trees > 22 cm dbh)	C. Steeger[5]	(Avail. = trees > 20 cm dbh)

[1] RH = relative height; mean height used/mean height available.

[2] Mean tree height of nests or nest trees/snags for all cavity nesters (P), and secondary cavity nesters (S).

[3] Tree Species Codes: TA = Trembling aspen; PB = Paper birch; BCo = Black cottonwood; DF = Douglas-fir; SPR = Spruce; WL = Western larch; WRC = Western red cedar; PP = Ponderosa pine; SF = Subalpine fir; WH = Western hemlock; LP = Lodgepole pine; GF = Grand fir; WP = White pine.

[4] Tree species used for nesting, but mean height available data were not provided.

[5] Unpublished data on file, Pandion Ecological Research, Nelson, British Columbia, Canada.

Table 5—*Selection of nest tree heights by height class. Selection is measured by Chesson's alpha (Chesson 1983).*

Height class (m)						**Source and Notes**
2-10	11-20	21-30	31-40	> 40		Nelson 1988 (snags)
0.00	0.02	0.07	0.14	0.76		
< 6	6-12	12-18	18-24	> 24		Madsen 1985 (snags)
0.05	0.25	0.18	0.14	0.37		
1.8-3.3	3.4-6.3	64-9.3	9.4-12.3	12.4-15.2	> 15.3	Schreiber & deCalesta 1992 (snags)
0.01	0.06	0.08	0.18	0.36	0.32	

Implications to Management

There are several ways to create either cavities or snags, but it is more practical to sustain them than to create them (Bunnell and others 1999). Creating high stumps produces snags that are used (Bennett 1994), but these are well below the heights sought by most birds and may encourage high rates of depredation. Although diameter appears a more reliable basis of management targets than height, there is no simple diameter limit. We offer two broad recommendations:

- *Sustain a range of diameters of decaying and dead trees.*

This recommendation follows from the range of diameters selected by cavity using species *(fig. 1).* Smaller snags provide some nesting opportunities, but, more importantly, they provide foraging sites (Bull and others 1986, Bunnell and others 2002). Many more foraging sites are needed than nesting sites.

- *Maintain some conifer snags of at least 50 centimeters diameter (30 centimeters in less productive forests).*

Because trees grown to provide cavities must rot and are not harvested, there is economic incentive to retain small trees. Earlier workers suggested minimum values derived from active snags as guidelines for snag retention (e.g., Connor and others 1975, Thomas and others 1979). Minimum values imply that most individuals are equally successful at nesting and reproducing at the lower ends of size distributions as those nesting at middle and high portions of the distribution. Available data suggest otherwise: while individual species nest in a wide range of tree or snag sizes, they tend to select larger ones when available *(tables 2, 3).* Cavity-nesters appear to select median sizes at which heart rot develops. The appropriate diameter is likely to be a function of tree species composition, species-specific rot patterns, and site.

Target diameters for nest trees should not be less than documented median diameters for the largest bird species present *(fig. 1).* Conifer trees must exceed 50 centimeters dbh to support all bird species *(fig. 1a).* Hardwood trees can be about 10 cm smaller *(fig. 1b).* Because studies have concentrated on forest types where trees are larger and more valuable, existing data overestimate requirements for areas where trees are smaller. A diameter > 30 centimeters likely will accommodate most bird species occurring in less productive forest types, but not the pileated woodpecker. A few mammals require still larger trees or snags (e.g., American marten, black bear), but need fewer of them than are required to sustain bird populations. Large trees and snags also have the advantage of standing longer than small snags (Graham 1981, Morrison and Raphael 1993).

Acknowledgments

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How Should We Spatially Distribute Dying and Dead Wood?[1]

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Abstract

We consider density and degree of aggregation of dead wood. Cavity nesters as a group respond asymptotically to snag density and attain half their maximum density at about 2.4 large snags/hectare. However, individual species show different responses, and there is no apparent effect of territoriality among smaller species. Dispersed retention of trees and snags strongly favors secondary cavity nesters and increases their abundance above that found in mature or old-growth forests; large patches favor primary nesters. Despite good operational and biological reasons for patchwise retention of dead wood, there are negative effects on some species.

Introduction

Many organisms rely upon dead wood (Bunnell and others 2002), and recent forest practices are exploring ways to sustain dead wood in managed stands (e.g., Anonymous 1995, Steventon and others 1998). There is a large literature on the sizes of dead trees and logs used by forest-dwelling organisms, but less is known about how that dead wood should be distributed within managed forests. We review relationships between forest-dwelling organisms and the amounts and distribution of dying or dead trees and dead wood on the ground. We focus on vertebrates, but briefly discuss other organisms that use dead wood. Our review is largely restricted to species of the Pacific Northwest defined as including Alaska, Alberta, British Columbia, Washington, Oregon, Idaho, Montana, and northern Nevada and California. References to other regions are included to indicate trends where forestry has been practiced longer, or where particular groups of species are well documented.

Density of Dying and Dead Trees

Richness and density of cavity-nesting birds are inconsistently related to snag densities. Studies surveying stands with many snags have obtained weak relations (e.g., Lundquist and Mariani 1991, Morrison and others 1987), while those including managed stands, in which some or all snags had been removed, have found stronger relations (e.g., Raphael and White 1984, Schreiber and deCalesta 1992). Bevis (1996)

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surveyed a range of stands from unmanaged to seed tree, and found the strongest predictor of red-breasted nuthatch *(Sitta canadensis)* and chickadee densities to be density of snags 25-50 centimeter dbh; $r^2 = 0.94$ and 0.83, respectively. These relationships may indicate nest site limitation, or they may reflect more productive foraging opportunities in stands with more snags (e.g., older stands with insect outbreaks versus thrifty managed stands).

Because rot within living trees is more common among hardwoods than among conifers, snag density is less important in hardwood stands. *Figure 1a* illustrates relationships for conifer stands with few hardwoods. Because much variation in cavity nester response to snag density is due to different size distributions of snags within stands, we limited estimates of snag density to larger snags that the birds use preferentially. Our diameter limits reflect the different sizes of preferred trees in coastal forests (about 50 centimeter dbh) and inland forests (30.5 to 38 centimeter dbh; Bunnell and others 2002). Bunnell and others (1999) fit a Michaelis-Menten relationship to the data *(fig. 1a)* under the assumption that the rate of response (cavity nesters density) was a function of the concentration of substrate (snags/hectare). The relationship implies an upper asymptote and a half-saturation constant. Response of the seven studies combined is asymptotic, with little additional increase in density of cavity nesters above about three large snags per hectare *(fig. 1a)*. Estimated parameters were an asymptote of 2.42 cavity nesting pairs/hectare and a half-saturation constant of 2.37 snags/hectare with an r^2 of 0.53. That shape is expected among territorial species limited by other resources. As the snag density increases, other required resources become more important factors in limiting bird density until finally the scarcity of other resources are completely limiting the bird density. Birds present at 0.0 snags per hectare indicate that some species can nest in snags < 30 centimeter dbh (some of them hardwoods, unreported in data on conifers). The response is consistently expressed, and each individual study of *figure 1a* shows an initial increase in cavity-nester density with increasing snag density.

Relationships for some bird species appear more linear *(fig. 1b,c)*. They suggest that competition for cavity sites is more strongly expressed within the entire cavity-nesting fauna than within the smaller species studied. Data of *figure 1c* also suggest that other habitat variables influence the response (compare data of Raphael and White 1984 with those of Cunningham and others 1980). We emphasize that smaller snags were present in all studies included in *figure 1*. Smaller snags are used as foraging sites, and foraging sites may be more often limiting than cavity sites (Walankiewicz 1991, Welsh and Capen 1992). More dead or dying wood than is required for nesting is needed to sustain all cavity-nesting species. Moreover, through provision of perching, foraging, and hawking sites, snags of all sizes tend to increase richness and abundance of birds other than cavity nesters (Dickson and others 1983, Scott 1979).

Species names mentioned in this text are taken from the following references: Plants—(Crittenden 1992); Birds—(Cannings and Harcombe 1990, Peterson and others 1993); Amphibians—(Cannings and Harcombe 1990); Mammals—(Cannings and Harcombe 1990, Whitaker 1993).

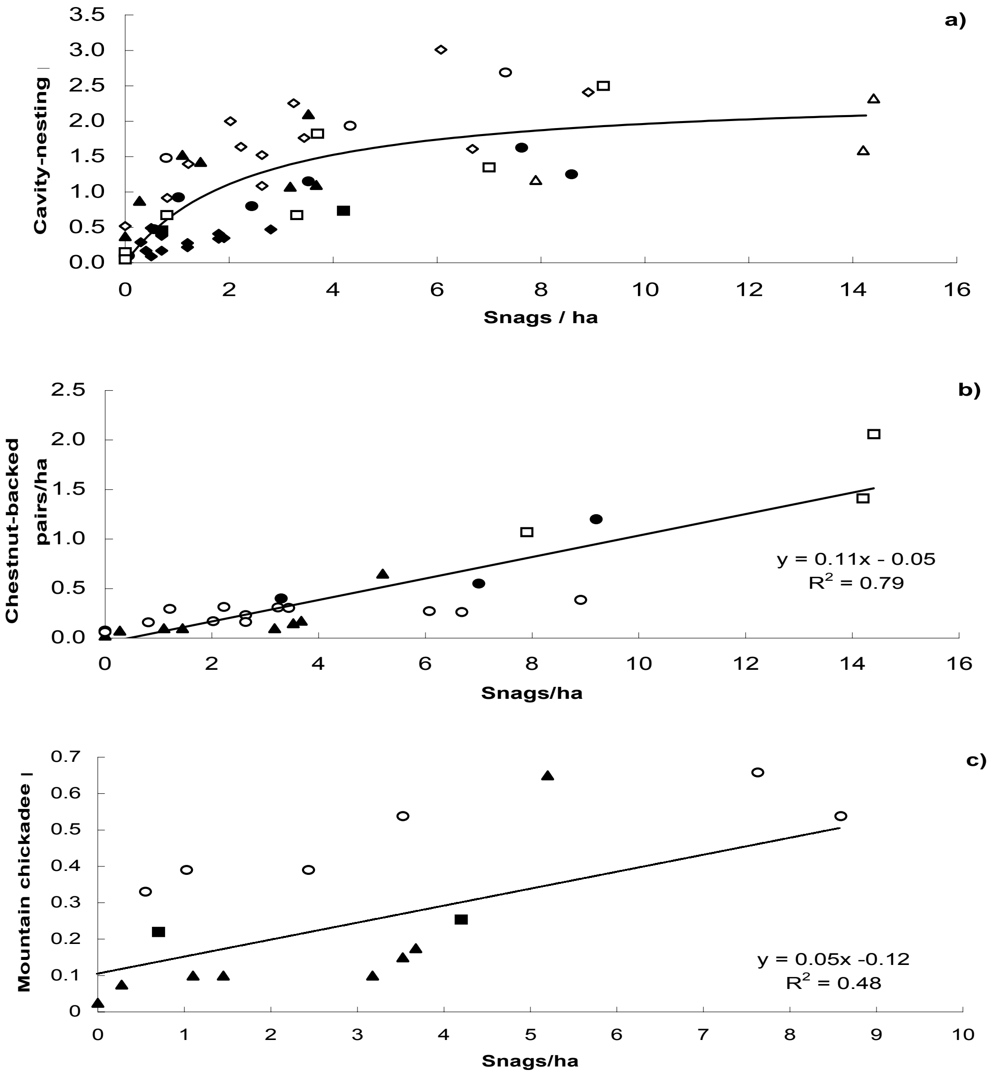

Figure 1—Density of cavity-nesting bird pairs versus snag density in primarily coniferous forests of the Pacific Northwest. Hollow symbols represent coastal forests; solid symbols are inland forest types. a) All cavity-nesting species. [**O**] = Carey and others 1991 (snags > 50 cm dbh); [▲] = Cunningham and others 1980 (snags > 30.5 cm dbh); [□] = Mannan 1977 (snags > 48 cm dbh); [■] = Mannan and Meslow 1984 (snags > 31 cm dbh); [◊] = Manuwal and Zarnowitz 1981 (snags > 51 cm dbh); [Δ]= Nelson 1988 (snags > 50 cm dbh); [●] = Raphael and White 1984 (> 38 cm dbh); [◆] = Steeger and Quesnel 1998 (snags > 50 cm dbh). Solid line is the fitted Michaelis-Menten relationship of the form cavity nesters per ha = 2.42 [asymptote] X (snags/hectare/ (snags/hectare + 2.37[half saturation constant])) (adapted from Bunnell and others 1999). b) Chestnut-backed chickadee pairs [▲] = Cunningham and others 1980 (snags > 30.5 cm dbh); [●] = Mannan 1977 (snags > 48 cm dbh). [**O**] = Manuwal and Zarnowitz 1981 (snags > 51 cm dbh); [□] = Nelson 1988 (snags > 50 cm dbh). c) Mountain chickadee (*Poecile gambeli*) pairs: [▲] = Cunningham and others 1980; [■] = Mannan and Meslow 1984; [**O**] = Raphael and White 1984.

Density of Downed Wood

The literature is least revealing of the appropriate amounts and distribution of downed wood. Of all habitat variables assessed, downed wood is the least consistently measured, and it is impossible to equate number of pieces, volume, and percent cover to extract broad patterns (e.g., Bunnell and Huggard 1999). In part, the variety of measurements reflects the fact that different ones are appropriate for different organisms: percent cover for some fungi, volume for terrestrial-breeding salamanders, and size for denning mammals. Although biologically appropriate, the variety prohibits synthesis. Moreover, when similar measurements exist, responses to downed wood within species are inconsistent, suggesting substitution with other habitat features, such as shrub cover (Bunnell and others 1999). Three broad points are evident from current data. First, hundreds of species in western forests are dependent upon decaying wood on the ground (Bunnell and others 2002). Second, volume of downed wood is important. That is most evident in data of Corn and Bury (1991) who reported that densities of clouded *(Aneides ferreus)* and western redback *(Plethodon vehiculum)* salamanders were relatively constant per cubic meter of downed wood, regardless of stand age. Third, some species seek out large pieces of downed wood, particularly marten *(Martes americana),* fisher *(Martes pennanti),* and black bears *(Ursus americanus)* (Bunnell and others 2002). Because these species also range more widely than most species using downed wood, required densities are probably low, provided scattered large pieces are accessible. In short, some downed wood is important for many species, and large pieces are critical to some.

Because different forest types grow and recruit different amounts of downed wood, it is misleading to transplant results. Initial studies have tended to focus on productive forests, which have little relevance to less productive forest types. What is clear is that size, decay class, and total amounts of downed wood have declined with the practice of forestry (e.g., Angelstam 1997, Spies and others 1988) to the detriment of many species (Berg and others 1994). In other words, we do not know what appropriate amounts are, but we do know we have not been recruiting enough downed wood (Bunnell and others 1997).

Distribution of Dying and Dead Trees

Effects of spatial arrangement of snags on cavity-nesters have received far less attention than the attributes of the individual nest trees (Swallow and others 1986). Dispersed retention of snags increased abundance and richness of secondary cavity nesters beyond that found in mature and old-growth forests, but abundance of primary nesters was much reduced *(fig. 2).* For primary cavity nesters, there are good reasons for retaining trees in patches. First, there is increased operational efficiency. Aggregated retention is safer during timber falling, especially when snags are retained, and windthrow is much reduced relative to dispersed retention or large clearcut edges (Coates 1997, Franklin and others 1997). Operational efficiency can also be gained in patches with a more desirable range of diameter and decay classes, that might prove difficult to select among the individual trees of dispersed retention. Aggregated retention also emulates natural patterns. Nests of primary excavators often are concentrated in dense patches of snags (Bull 1980, Lundquist and Mariani 1991, Raphael and White 1984). It is unclear whether this implies selection of dense patches for some associated value (e.g., social facilitation) or merely reflects the patchy way in which trees are killed by insects or disease. Cavity sites often are concentrated where rots are concentrated in both hardwoods (e.g., *Phellinus* in aspen *[Populus tremuloides]* and birch *[Betula papyrifera];* Merkens and others 1996), conifers (e.g., *Armillaria* in Douglas-fir *[Pseudotsuga menzieseii]),* and lodgepole pine *(Pinus contorta;* Steeger and Hitchcock 1998).

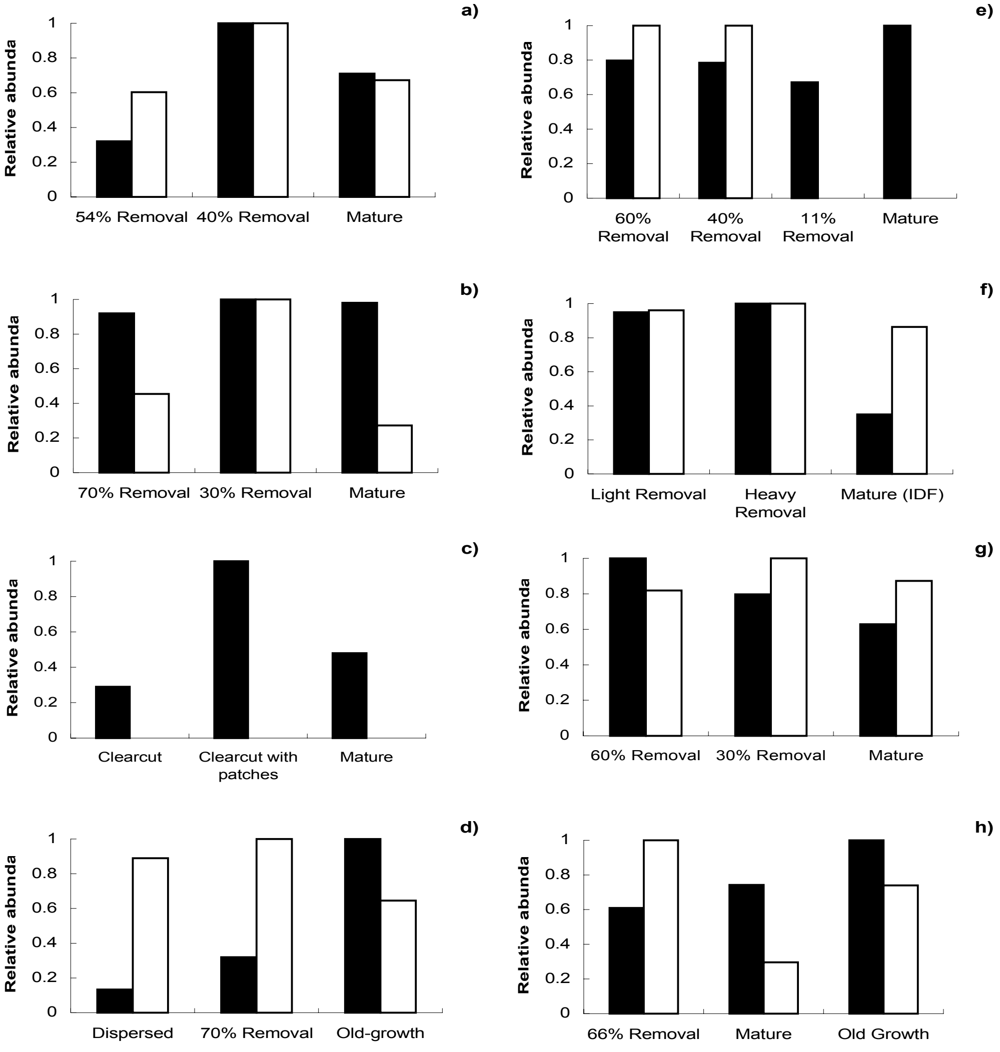

Figure 2—Relative abundance of primary [■] and secondary [□] cavity nesters in different forms of partial harvest. Data sources are a) Scott and Oldemeyer (1983) in Ponderosa pine (*Pinus ponderosa*). b) Steeger and Quesnel (1998) in interior Douglas-fir. c) Gyug and Bennett (1996) in interior western redcedar-hemlock; see text for patch sizes. d) Bryant (1997) in coastal western hemlock; dispersed retention retained about 25 trees per ha. e) Waterhouse and Dawson (1999) in interior Douglas-fir. f) Morgan and others (1989) in interior Douglas-fir; amount removed unspecified. g) Steventon and others (1998) in interior western redcedar-hemlock, h) Tobalske and others (1991) in western larch-Douglas fir.

The most compelling reason for aggregated retention of wildlife trees is that it has been shown to be effective when larger patches are retained. The utility of small patches appears undocumented, but Gyug and Bennett (1996) studied large seed-tree reserves in clearcuts 25 to 29 years after harvesting. Patches retained in the 160 hectare clearcut averaged 0.9 hectare (range 0.3 to 1.5 hectare); in the 1,000 hectare clearcut they averaged 3.6 hectares (range 1.6 to 18.9 hectares). Combined, the patches represented 7 to 10 percent of the gross area. In both clearcuts, more primary cavity nesters were detected in the patches than in the nearby forest, including pileated *(Dryocopus pileatus)* and hairy *(Picoides villosus)* woodpeckers. Current data also suggest that various silviculture systems that maintain some cover somewhere at all times (continuous-cover) are effective at sustaining cavity nesters *(fig. 2)*.

Two broad patterns are evident. First, in all studies of *figure 2*, secondary cavity nesters were higher in areas experiencing some timber removal than in mature or old-growth forests. That increase likely reflects the fact that many secondary nesters forage more effectively in openings. Second, in most instances the abundance of primary cavity nesters was little affected by partial harvesting, and in some instances increased in abundance. That may reflect the fact that several primary excavators also favor small openings and edges (e.g., hairy woodpeckers; Klenner and Huggard 1998; northern flicker *[Colaptes auratus],* Campbell and others 1990; three-toed woodpecker *[Picoides tridactylus],* Klenner and Huggard 1997; and perhaps downy woodpecker *[Picoides pubescens],* Petit and others 1985). For three-toed woodpeckers, Klenner and Huggard (1997) noted that preferred nest sites were within 20 meters of an edge. If regulations encourage snag removal near edges, patches must be larger and continuous-cover systems will be less effective.

Distribution of Downed Wood

Downed wood can be provided by leaving slash or logs after harvest or by retaining trees to fall to the ground and become downed wood. Slash, including logs, can be either dispersed over the cutblock or aggregated into piles or windrows. More information is available on aggregated retention of downed wood than on dispersed retention.

Several species of small mammals use piles of both fine and coarse logging debris, including red-backed voles (*Clethrionomys* spp.), martens, and short-tailed weasels *(Mustela erminea)* (Lisgo 1999, Morris 1984, Raphael and Jones 1997). Jones and Raphael (1995) described 32 maternal den sites of marten in Oregon: 10 were in slash piles, 10 in logs, 6 in snags, 5 in live trees, and 1 in a stump. Using winter tracking, Gyug (1993, 1994) found that marten use of clearcuts without debris was very low compared to use of adjacent forests. Use of clearcuts with debris piles was significantly higher, but still lower than in adjacent forest. Isolated debris piles were not used by marten unless they were on a path of 135 meters or less between adjacent forest cover. Lisgo and others (2002) documented similar responses of weasels to debris piles in the boreal mixedwood of Alberta. Although marten and weasels hunted around debris piles, small mammal responses to debris were inconsistent. Gyug (1994) found that the presence and number of debris piles did not significantly increase the number of most small mammals. Red-backed voles were almost absent from clearcuts except in piles within 40 meters of forest edges, and only common shrews (*Sorex* spp.) were significantly more abundant when debris piles were present. Lisgo and others (2002) found greater abundance of small mammals around slash piles than in clearcuts, particularly for red-backed voles. Benefits of piling logging residues remain unclear, because current data simply report higher densities of small mammals in piles than in clearcut areas without piles. Responses to dispersed downed wood have not been compared with aggregated downed wood.

For some organisms, dispersed retention of logging residues is advantageous. Because conditions of stable high humidity are favorable for bryophytes (Sharp 1939), particularly liverworts (Söderström 1988), the humidity and moisture content of logs are especially important to bryophytes (Andersson and Hytteborn 1991). Forest floor bryophytes generally have limited dispersal ability (Khanna 1964, Söderström 1987), and dispersal is from log to log. For these reasons, Samuelsson and others (1994) argued that logs should be close together, but not gathered into piles. It is probable that other organisms whose favored, or only, habitat is downed wood also are poor dispersers. Amaranthus and others (1994) and Carey and Johnson (1995) found that the abundance of truffles and truffle-like fungi, was related to the amount of forest floor covered by logs. More forest floor is covered if the logs are not piled. Encouraging truffles and truffle-eating mammals is a sensible thing to do if sustaining forest productivity is a goal (Harley 1969, Marks and Kozlowski 1973, Maser and others 1978). A dispersed distribution of downed wood would help to disperse both small mammals and mycorrhizae across the site.

There are tradeoffs between aggregating logging residuals or leaving it dispersed. Aggregations are used by several small mammals, both predator and prey. More evenly dispersed retention favors some fungi as well as bryophytes restricted to downed wood. Because there is not an unequivocal best way to distribute logging residuals, the wisest approach is not to do the same thing everywhere.

The other approach to providing downed wood is through dispersed or aggregated retention of living trees. Retained trees die a natural death and likely will have incurred fungal invasion. Natural cavities from heart rot are more likely, and invertebrates associated with some fungi are more likely to survive. Higher windthrow rates in dispersed retention hasten the provision of downed wood, but reduce the period when these trees can provide cavity sites. As well as reduced susceptibility to windthrow, aggregated retention of older trees (patches) has the advantage of immediate provision of downed wood. Additional advantages to aggregated retention are those noted with respect to cavity users, notably the provision of a range of decay and size classes. The disadvantage is that such provision is clearly not dispersed across the landscape. Species restricted to downed wood and that disperse poorly will be disadvantaged.

Implications to Management

From this review, we offer the following recommendations for the distribution of dead wood in managed forest:

- Maintain a target density of 2-3 large snags (> 50 or 30 centimeter diameter) per hectare, among 10-20 smaller snags per hectare through the rotation. However, ensure variation in densities, not an even distribution everywhere.

Cavity sites can become limiting, and there is a density below which species disappear (Campbell and others 1990, 1997; Newton 1994). Data of *figure 1* suggest that in conifer types little is gained by sustained provision of more than about three large snags per hectare (> 50 centimeter dbh in coastal forests; > 30 centimeters in less productive forests). More smaller snags must be present, both as foraging sites and because some species find cavity sites in small snags. There are no applicable data, but we estimate 10 to 20 smaller snags per hectare as appropriate. In hardwood types, there is little need for a target density of snags, because most cavity nests are found in living trees. Providing for future recruitment of snags in coniferous stands is necessary to ensure that target densities are maintained through the rotation and after harvest. Suggested densities do not apply to each hectare of forest. Because of the diversity of organisms using snags, variability in density of snags must be maintained within and among stands.

- Amounts of downed wood?

Logs as small as 6 centimeters are favorable to shrews (Craig 1995), but in some forest types larger mammals prefer significant amounts (100 to 200 cubic meters/hectare or more) and sizes (> 50 centimeter diameter) of downed wood (review of Lofroth 1993). Current data suggest little more than small amounts are useful but that mammals such as marten, fisher, and black bear require scattered, large pieces, 50 to 100 centimeter diameter.

- Patches of 1-3 hectares will sustain some smaller species, even in extensive clearcuts.

Such patches sustain most, if not all, cavity nesters *(fig. 2)*. Home ranges of some terrestrial-breeding salamanders and shrews are small enough (Craig 1995, Nussbaum and others 1983) that groups of individuals can be sustained within 1 hectare; 3 hectares will sustain groups of rodents (e.g., Mahon 1998, Thompson 1996). Retention of some logs on site would permit them to recolonize larger areas.

- Retaining snags in moderate-sized patches has several advantages. It should not, however, be the only distribution of snags used.

Retention of trees in patches helps reduce safety risks of snag retention, provided patches are large enough. Aggregates of 1-3 hectares are used by cavity-nesters in large openings, and are practical where snag-falling regulations permit snag retention within them. Aggregated retention also reduces risks of windthrow and provides diverse nesting opportunities over a range of size and decay classes. Although aggregating retention in moderate-sized patches has advantages, it should not be the only approach used. Dispersed retention of snags, or declining live trees intended to become snags, may be particularly advantageous for perching birds, and for territorial secondary users, such as raptors, and some small birds. Dispersed retention, however, may impact shrub nesters (Vega 1993) and should not be used everywhere.

Continuous-cover systems, such as individual tree selection, group selection and small (0.1-3 hectare) patch cut arrays have a number of benefits *(fig. 2),* and are of increasing operational interest (Vyse 1999). Openings of up to 3 hectares appear to have little effect on primary cavity nesters when 50 percent of the older forest is retained (Bryant 1997). However, repeated entries and need to fall snags in the surrounding forest can eliminate snags from large areas (Huggard 1997). Aggregated reserves should be considered for snag management in these systems.

- Meet dead wood requirements for larger species in areas where the emphasis is not on intensive fiber production.

The economic and ecological advantages of zoning intensity of forest practices (Binkley 1997, Bunnell and others 1999) suggests that needs of species requiring large amounts of dead wood are best provided in areas where late-successional attributes are being maintained. Most (perhaps all) of these species use clearcuts to forage and often find preferred food there, but must have denning sites nearby. Provision of large amounts of downed wood within clearcuts is incompatible with profit incentives of intensive fiber production.

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Evaluating the Effects of Partial Cutting on Wildlife Trees and Coarse Woody Debris[1]

Susan K. Stevenson[2] and Dagmar G. Keisker[3]

Abstract

In the wet forests of interior British Columbia, Canada, partial cutting can be used to produce stands that resemble natural uneven-aged forests. We have begun a long-term study of the effects of several partial cutting prescriptions on structural attributes and ecosystem processes in these forests. We employ a new classification of functional types of wildlife trees and coarse woody debris. A "Type" is a configuration of habitat features required by one or more wildlife species for specific functions. We present preliminary data on the occurrence of Wildlife Tree and Coarse Woody Debris Types before and after partial cutting in a fir-spruce stand.

Introduction

The existence of a major conference devoted to the ecology and management of dead wood indicates a recognition of the ecological importance of dead wood, and a desire to maintain in managed stands the functional processes that it supports. This is part of a larger recognition that the structures and processes that occur naturally are important to maintaining the biodiversity and productivity of forests, and furthermore that those structures and processes will not necessarily survive in managed stands unless special efforts are made to maintain them.

Using selection silvicultural systems in forests that are naturally uneven-aged is one approach to maintaining natural structures and processes in managed stands. The interior wetbelt of British Columbia, Canada, is an area of high precipitation and low fire frequency located on the windward side of the Rocky Mountains. It is dominated by western red cedar *(Thuja plicata* Donn) and western hemlock *(Tsuga heterophylla* [Raf.] Sarg.) at low elevations and Engelmann spruce *(Picea engelmannii* Parry) and subalpine fir *(Abies lasiocarpa* [Hook.] Nutt.) at higher elevations. Many stands are naturally uneven-aged. In the interior wetbelt there is increasing interest in selection silvicultural systems both for ecological reasons and to meet specific management objectives, such as conserving habitat for mountain *caribou (Rangifer tarandus caribou* Gmelin) or protecting scenic quality.

A research group at the University of Northern British Columbia has begun a long-term replicated study of the effects of several partial cutting systems on a

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variety of structural attributes and ecosystem processes, including the loss and creation of wildlife trees and coarse woody debris (Jull and others 2001). That component of our study focuses on comparing the occurrence of damage agents and of structural attributes that are important to wildlife in undisturbed and post-harvest stands. We employ a new classification of functional types of wildlife trees and coarse woody debris. Our objectives in this paper are to describe the new classification system of wildlife habitat features associated with standing and fallen trees, and to present preliminary results of a pilot project that evaluates the short-term effects of partial cutting on those habitat features.

Background

In recent years, increased scientific understanding of the ecology of natural disturbances has led to a paradigm shift in forest management (Rogers 1996). Forest managers have often viewed disturbances negatively and tried to suppress them. Many of those attempts, such as fire suppression and insecticide application, have had unanticipated negative consequences of their own (Rogers 1996). The disturbances themselves have been shown to have a key role in supporting the ecosystem processes essential to forest productivity and biodiversity. Increasingly, managers have come to view disturbances as natural processes that must be maintained if we wish to maintain ecological integrity.

Furthermore, many scientists and managers today see natural disturbance regimes not only as natural processes of value, but as models for forest management regimes. British Columbia's *Biodiversity Guidebook* states as its first principle, "The more that managed forests resemble the forests that were established from natural disturbances, the greater the probability that all native species and ecological processes will be maintained" (Ministry of Forests and British Columbia Environment 1995).

In the interior wetbelt of central British Columbia, stand-initiating fires occur infrequently. The common means of natural forest regeneration are small disturbances in which one or a few trees are killed by insects, disease, or windthrow. The resulting canopy gaps, standing dead trees, and coarse woody debris have a pervasive influence on the ecology of wet forests, including tree recruitment, understory vegetation dynamics, wildlife habitat, stream structure and dynamics, biomass dynamics, and carbon budgets (Lertzman and others 1996). Whereas clearcut silvicultural systems can mimic the effects of stand-destroying fires, partial-cut silvicultural systems are better suited to maintain the uneven age- and size-class distributions and the structural attributes that result from a natural disturbance regime dominated by small-scale mortality events.

However, selection harvested stands differ from natural stands in several important ways, some of which may affect the stands' ability to provide important structures and processes. Felled trees are removed from the block rather than remaining on the forest floor. For economic reasons, it is often necessary to remove more trees in a single entry than would die naturally at any one time. Trees that could be dangerous to forest workers must be felled, even if they are unmerchantable. Over time, there is likely to be an increase in the amount of young wood and a decrease in the amount of old or dead wood.

The landscape pattern that results from logging may be conceptualized as a secondary mosaic of disturbance overlaying nature's disturbance patterns (Ripple and others 1991). Regardless of whether or not the human-caused disturbance pattern resembles the natural disturbance pattern, the natural agents of disturbance continue to operate. However, the frequency, severity, and character of those natural disturbances may be affected by forest harvesting.

Although disturbance ecology is currently an active area of research, we are aware of little work on the effects of harvesting on natural disturbance agents in the residual stands after partial cutting. Relationships have been documented between silvicultural systems and the occurrence of specific disturbance agents, such as western spruce budworm (Carlson and Schmidt 1989), windthrow (Coates 1997), and decay organisms and insects (Nevill and Whitehead 1996). But there seems to be little information on how the overall assemblage of disturbance agents is affected by partial cutting.

In the interior wetbelt of central British Columbia, trees that have been damaged by disturbance agents provide a rich variety of habitats for the 61 vertebrate species that are obligate or frequent users of wildlife trees, and the 51 vertebrate species that are obligate or frequent users of coarse woody debris (Keisker 2000). The habitat values of these trees and logs are linked to the damage agents that have affected them. If different silvicultural systems result in different levels of occurrence of various damage agents, they may also result, over time, in different levels of occurrence of the wildlife habitat attributes associated with damaged or dead trees. One of the objectives of the research of Jull and others (2001) is to find out how various partial-cutting prescriptions affect the assemblage of disturbance agents and the occurrence of standing trees and coarse woody debris with wildlife habitat attributes.

Study Area

The study area for the pilot project is located at Pinkerton Mountain, about 90 km east-southeast of Prince George, British Columbia, Canada, in the Engelmann Spruce-Subalpine Fir zone (Meidinger and Pojar 1991). The mesic to subhygric site is on a southwest-facing slope at 1,350-1,470 m a.s.l. Pre-harvest basal area was approximately 35 m^2/ha, composed of 78 percent subalpine fir and 22 percent Engelmann spruce.

Harvesting Methods

The study area comprises a 40-ha single tree selection unit, a 59-ha group selection unit, and a 25-ha unharvested control area. The target level of volume removal in both units was 30 percent. In the group selection unit, the trees were removed in openings that ranged from 0.1 to 0.4 ha. In the single tree selection unit, trees to be cut were marked to leave a target diameter distribution with relatively high retention of large trees. The block was logged in early 1998 on a late winter snowpack by mechanized harvesting machines. The harvesting was described in more detail by Stevenson and others (1999).

Study Methods

Sampling was based in and around 14 systematically located permanent sample plots, 7 in each of the 2 treatment areas. At each location, a 0.05-ha plot was nested inside a 0.10-ha plot. In the inner plot, all standing trees $\geq$ 10 cm dbh were assessed, and in the outer plot all trees $\geq$ 25 cm were assessed. In addition to standard mensurational data, we recorded damage agents, evidence of wildlife use, and Wildlife Tree Types and two Coarse Woody Debris Types for each sample tree.

Coarse woody debris was tallied along at least two 24-m transects associated with each permanent sample plot. For each piece, we recorded various standard data (Ministry of Forests 1997) and Coarse Woody Debris Types.

Trees and coarse woody debris were assessed in summer 1997 and again in summer 1998, after logging was completed. Some trees that were standing after the harvest were potentially dangerous to workers and should have been removed according to the safety regulations of the Workers' Compensation Board (WCB) of British Columbia (Stone and others 2001). To ensure that the data represented realistic conditions, such trees were omitted from the analysis.

Because of unequal sample sizes between treatment units and before and after logging, results are shown as percentages of the number of sample trees or logs in each treatment unit exhibiting a given attribute. The log-likelihood ratio *G* (Sokal and Rohlf 1995) was used as a test statistic to compare the frequency distributions of the number of Types associated with each sample tree or log in the two treatment units. Assessments carried out in the control area are not reported here.

Wildlife Tree and Coarse Woody Debris Types

Our classification system of habitat features associated with wildlife trees and coarse woody debris is based on the concept of the "Type"—a configuration of habitat features that appears to be required by one or more wildlife species for specific functions (Keisker 2000). The classification developed from a project in which available information on wildlife habitat requirements involving wildlife trees and coarse woody debris in the north-central interior of British Columbia was reviewed and presented in a summary format that would be useful to managers (Keisker 2000). For that purpose, information was condensed by including only those habitat features that have functional significance to wildlife and by delineating sets of these features, termed "Types," that serve specific functions for groups of wildlife.

Ten Wildlife Tree (WT) Types and six Coarse Woody Debris (CWD) Types were described by Keisker (2000) and are summarized in *tables 1* and *2*. The term "wildlife tree" refers to a standing dead or live tree with special characteristics that are valuable for wildlife and that distinguish it from most other trees in the forest. The sets of features that define the Types are often not mutually exclusive. A single tree or CWD piece may have 0, 1, or more Types. Although the Types were developed for wildlife species and ecosystems occurring in the north-central interior of British Columbia, we believe that both the approach and the results have a broader geographic applicability.

CWD Types 1, 2, and 3 may apply to standing trees as well as logs. We included CWD-1 and CWD-3 in our assessments of standing trees, but not CWD-2, because it applied to almost every tree.

Table 1—*Types of Wildlife Trees required by wildlife of north-central British Columbia (Keisker 2000).*

Main function		Type	Main users
Reproduction/resting:			
Substrates for cavity excavation	WT-1	Hard outer wood surrounding decay-softened inner wood	Woodpeckers (stronger excavators)
	WT-2	Outer and inner wood softened by decay	Woodpeckers (weaker excavators), chickadees, nuthatches
Existing cavities	WT-3	Small, excavated or natural cavities	Chickadees, nuthatches, swallows, bats
	WT-4	Large, excavated or natural cavities	Ducks, owls, bluebirds, swallows, bats, squirrels, mustelids
	WT-5	Very large natural cavities or hollow trees	Swifts, owls, bats, mustelids
	WT-6	Cracks, loose bark, or deeply furrowed bark	Creepers, bats
Large open-nest supports and other non-cavity sites	WT-7	Witches' brooms	Diurnal raptors, owls, squirrels, mustelids
	WT-8	Large branches, multiple leaders, or large-diameter broken tops	Herons, diurnal raptors, owls
Foraging:			
Feeding substrates	WT-9	Arthropods in wood or under bark	Woodpeckers
Hunting perches	WT-10	Open-structured trees in or adjacent to open areas	Diurnal raptors, owls

Table 2—*Types of coarse woody debris (CWD) required by wildlife of north-central British Columbia (Keisker 2000).*

Main function		Type	Main users
Reproduction/resting /escape:			
Concealed spaces	CWD-1	Large concealed spaces	Grouse, hare, woodrat, porcupine, fox, cats, some mustelids, bears
	CWD-2	Small concealed spaces (or soft substrate allowing excavation of such spaces) at or below ground-level beneath hard material	Salamander, toad, treefrog, snakes, wrens, shrews, voles, deer mouse, golden-mantled ground squirrel, chipmunk, jumping mice, weasels

	CWD-3	Small concealed spaces above ground-level	Treefrog, Yellow-bellied Flycatcher, wrens, Townsend's Solitaire, some wood warblers, some sparrows
Travel:			
Concealed runways	CWD-4	Long concealed spaces (or soft substrate allowing construction of runways)	Salamander, some snakes, wrens, shrews, voles, deer mouse, weasels
Exposed, raised travel lanes	CWD-5	Large or elevated, long material clear of dense vegetation	Tree squirrels, chipmunk
Foraging:			
Feeding substrates	CWD-6	Invertebrates in wood, under bark or moss-cover, or in litter/humus accumulated around CWD	Salamander, treefrog, woodpeckers, wrens, some sparrows, shrews, deer mouse, skunk, bears

Results and Discussion

Two of our main interests in this pilot project were to learn about the frequency of occurrence of the various WT and CWD Types in a high-elevation fir-spruce stand, and to obtain a preliminary indication of the different effects of group and single tree selection. We expected that the two different partial cutting prescriptions would have different effects on the occurrence of WT Types, but not necessarily CWD Types. According to worker safety regulations, if work in a forestry operation will expose a worker to a dangerous tree, that tree must be removed (Stone and others 2002). Harvesting is dispersed throughout a single tree selection unit, and many of the danger trees are potentially subject to removal. In a group selection unit, work activity is more concentrated, and more of the danger trees are likely to be located away from work areas. Because wildlife tree attributes are often associated with damage or decay that could make a tree dangerous, we expected that fewer trees with WT Types would be retained in the single tree selection unit than the group selection unit.

Most WT Types were uncommon in the study area before harvesting, occurring with a frequency of less than 5 percent *(fig. 1)*. Fifteen to 20 percent of the sample trees had large concealed spaces at or below ground-level (CWD-1), possibly because they had originated on nurse logs which had subsequently rotted away. Loose bark or wide cracks (WT-6) were also common (15-20 percent). Hunting perches (WT-10) were moderately common (5-10 percent) in this high-elevation stand, which had many natural gaps. WT-10 was recorded more often in the unit assigned to group selection than the unit assigned to single tree selection (G = 11.114; df = 1; p = 0.001), although refinements to the identification criteria for that Type that were made during sampling may have contributed to the difference. No other differences were found between the pre-harvest occurrence of the other Types in the two treatment units.

Because the planned level of volume removal was 30 percent throughout the harvest block, we expected that the proportion of sample trees remaining after harvesting would be similar in the two treatment units. In fact, however, harvested areas were overrepresented in the group selection sample plots. Of those seven plots, one was completely logged, one was completely unlogged, and five were partly logged, but only 42 percent of the original sample trees were still present. In the single tree selection unit, some trees had been felled in all the plots except one, which was located on a short, steep slope; and 67 percent of the sample trees remained after logging. Because of the difficulty of obtaining adequate representation of harvested and unharvested areas in non-uniform treatment units, we will use a stratified sampling scheme in future studies.

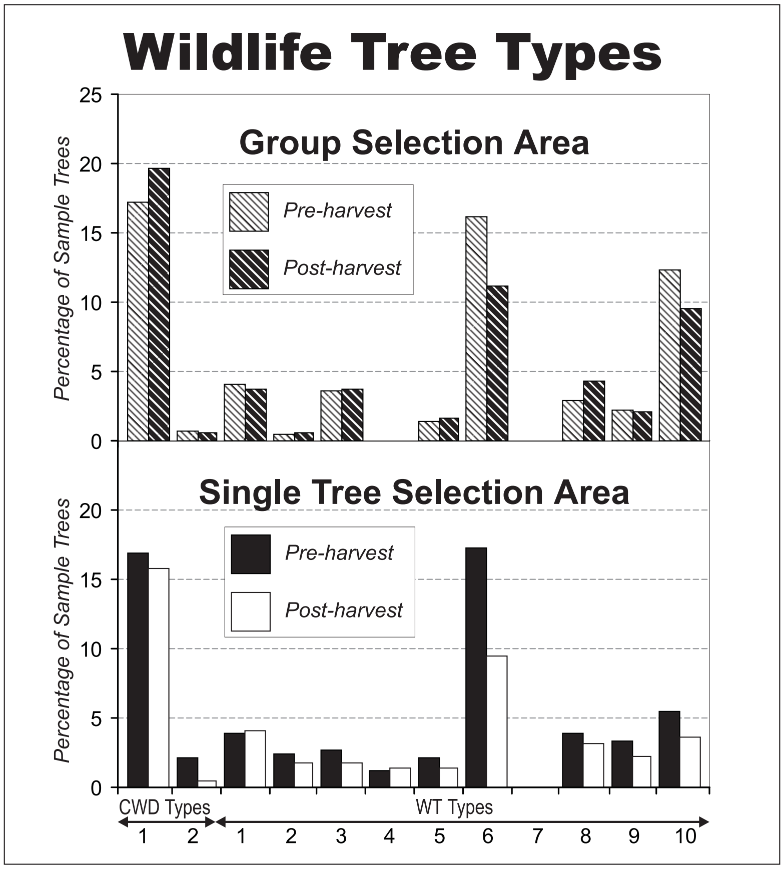

Figure 1—Occurrence of 10 WT and 2 CWD Types associated with standing trees before and after group selection and single tree selection logging at Pinkerton Mountain, British Columbia.

Our primary interest was not in the number of trees that remained after logging, but in the habitat attributes of those trees. The proportion of sample trees with Types did not change as much after harvesting as we had expected, nor was there a pronounced difference between the two treatment units. The most conspicuous reduction was in the occurrence of WT-6. In our study area, loose bark or wide cracks were usually associated with hard subalpine fir snags that had been dead for some time (Stage 4 of Thomas 1979). These trees were commonly dangerous and often had their full height, which made them more likely than shorter trees to affect work areas. Aside from WT-6, occurrence of Types was similar or only slightly reduced after harvesting.

The results shown in *figure 1* are inconvenient for statistical analysis because the number of observations in some categories is very small, the categories are not ordered, and it is not reasonable in most cases to increase the number of observations by grouping categories. We used the number of Types associated with each sample tree as a single variable to characterize the habitat value of that tree, and the frequency distribution of the number of Types to characterize the stand. Before the harvest, 35.8 percent of the 776 sample trees in the 14 plots exhibited one or more Types, and the frequency distributions of number of Types in the two treatment units did not differ (*G* = 3.995; df = 4; p = 0.407). After harvesting, 30.6 percent of the 409 remaining sample trees had one or more Types, and the frequency distributions were still not significantly different (*fig. 2; G* = 5.900; df = 4; p = 0.207).

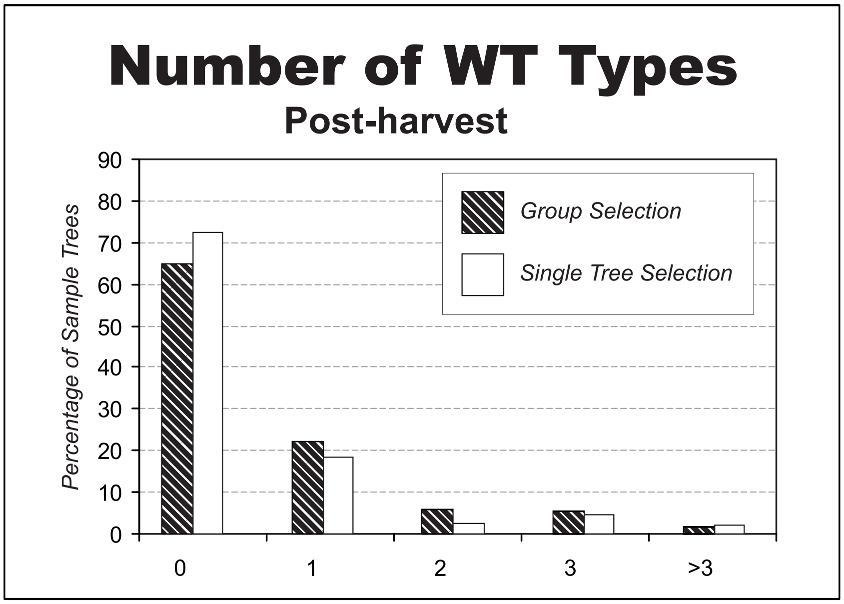

Figure 2—Frequency distribution of the number of WT and CWD Types associated with standing trees after group selection (GS) and single tree selection (STS) at Pinkerton Mountain, British Columbia.

The relatively high retention of trees with Types after partial cutting and the small differences between the group selection and single tree selection units were unexpected. We found that some Types occurred in trees that were not dangerous to workers, either because the attribute was not associated with any structural defects that made the tree hazardous, because the tree was short enough that it would not affect any work areas, or because a tree that was otherwise hazardous was buffered from work areas by healthy green trees that would break its fall. Also, we found that even in the single tree selection unit, there were areas where no logging took place, either because they could not easily be accessed or because initial basal area was low and no trees had been marked for cutting.

Unlike WT Types, CWD Types are very common. Ninety percent of the 397 pieces that were tallied in pre-harvest plots had one or more CWD Types. CWD Types 1, 2, and 4 were the most common, occurring consistently in more than 20 percent of the sample pieces. Occurrence of the various Types was similar before and after harvest in both treatment units, except for an apparent increase in CWD-1—large concealed spaces—after harvesting in both units. There may have been more spaces around and under logs where logging residue had been piled.

Because CWD Types are common, the frequency distribution of number of CWD Types *(fig. 3)* has a different shape from that of the WT Types *(fig. 2)*. Frequency distributions of CWD Types did not differ between treatment units either before harvesting (G = 7.358; df = 5; p = 0.195) or after harvesting (G = 3.079; df = 5; p = 0.688).

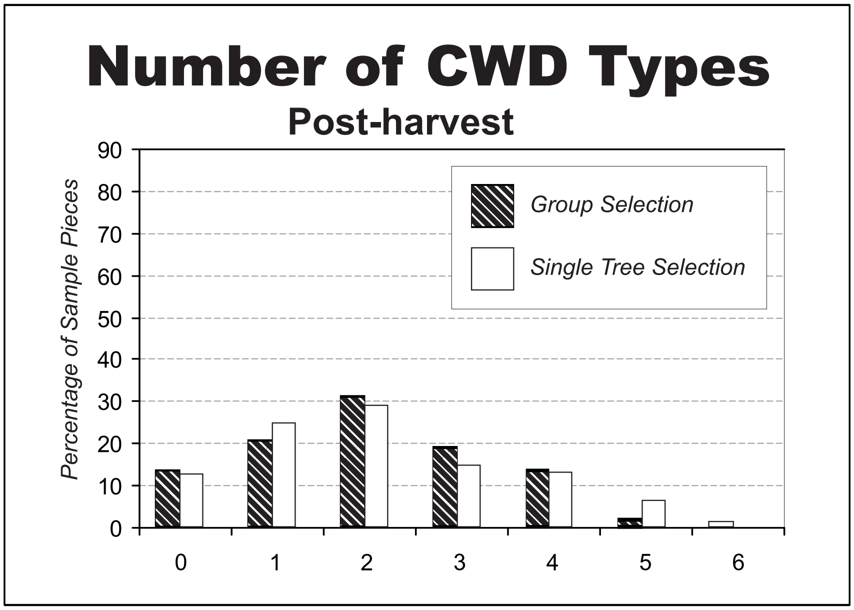

Figure 3—Frequency distribution of the number of CWD Types associated with down logs after group selection (GS) and single tree selection (STS) at Pinkerton Mountain, British Columbia.

The results of this pilot project have limitations that restrict their generality: only one site was studied, sample sizes were small, and the treatments were not randomly assigned. The results described here should not be extrapolated to other sites. However, the approach has broad applicability when used in a larger, replicated experimental design.

Conclusion

The preliminary results of this pilot project suggest that, at least in some cases, selection harvesting may have little impact on the percentage occurrence of the attributes of standing trees and coarse woody debris that are most important to wildlife. However, it would be premature to base any conclusions on an unreplicated study in which sample sizes were small and methodological problems were still being resolved.

The classification system of WT and CWD Types described here appears to be a useful tool with which to evaluate the effects of various silvicultural systems in both the short-term and the long-term. We would expect that with larger sample sizes we might find that some Types, such as WT-6, are more likely than others to be substantially reduced by partial cutting. Different methods of partial cutting, such as helicopter logging, cable logging, and hand-felling, may affect the occurrence of WT and CWD Types differently. We would also expect that the patterns of occurrence of the various Types will vary with the age and species composition of forest stands. Eventually, the results of these studies should help managers to plan how to maintain the full array of structural attributes that are critical to wildlife.

Acknowledgments

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Created Snag Monitoring on the Willamette National Forest[1]

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Abstract

Management agencies currently create snags from live trees and leave them in stands after cutting. Little information exists on the use of these snags by wildlife. This study had two objectives: to document whether created snags were used by wildlife, and if used, to elucidate stand and snag features associated with the use of these created snags by wildlife. We documented sign of woodpecker foraging and/or nesting or roosting use, along with snag and stand features in 55 systematically selected stands across the Willamette National Forest in Oregon. We found that woodpecker use was associated with created snag characteristics. Mainly, the status (live or dead) of the created snag was associated with the presence or absence of woodpecker foraging excavations. Management considerations are discussed, including the need to monitor wildlife use before and after created snags are killed and in subsequent years.

Introduction

Standing dead trees (snags) are important resources for vertebrate and invertebrate species worldwide and to forested ecosystems. They return essential nutrients to the soil and increase soil fertility. Throughout North America, over 85 species of birds use snags for nesting, foraging, or drumming (Raphael and White 1984, Scott and others 1977). In the Douglas-fir *(Pseudotsuga menziesii)* and western hemlock *(Tsuga heterophylla)* forests of the Pacific Northwest, over 100 vertebrate species utilize snags for some part of their life cycle (Neitro and others 1985, Thomas and others 1979). Approximately 20 percent (34 species) of all bird species in the Pacific Northwest depend on snags for nesting and feeding (Carey and others 1991, Lundquist and Mariani 1991). Furthermore, the abundance of snag-dependent birds has been shown to be correlated with the density of suitable snags (Carey 1995, Scott 1979, Stribling and others 1990, Zarnowitz and Manuwal 1985). Also populations of northern flying squirrel *(Glaucomys sabrinus),* the primary prey item of the threatened northern spotted owl *(Strix occidentalis caurina)* reach their highest densities in forests with large snags (Carey 1995).

Despite current widespread understanding of their importance for wildlife, and their prevalence in natural forested systems (Carey and others 1991, Ohmann and others 1994, Spies and Franklin 1991, Spies and Thomas 1988, Tyrrell and Crow 1994a, 1994b), snags have been systematically eliminated from managed landscapes

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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for several decades (Carey 1995, Zarnowitz and Manuwal 1985), due to concerns about the role that snags may have in creating conditions suitable for fires, insect outbreaks, and as hazard trees. Within the past 15 years, however, most State and Federal and some private land management agencies have devised strategies to maintain, and in some cases enhance, snag abundance on their lands (USDA and DOI 1994).

Ways to enhance habitat for snag dependent wildlife are being tested by blasting or sawing the tops off of living trees; girdling live trees; inoculating live trees with fungus; and inducing bark beetle attacks. During the past 15 years, management plans on the Willamette National Forest (WNF) in western Oregon have required that varying levels of natural and artificially created snags be retained in units that are harvested for timber (USDA and DOI 1994). While snags have been artificially created by all three methods on the WNF, the vast majority have been artificially created by blasting and sawing off tree tops. At this time, however, very little information exists on the use of these artificially created snags by wildlife (Chambers and others 1997), or on the decay and fall-down rates of artificially created snags.

To address this lack of information, we began a long-term monitoring project in the summer of 1997. The objectives of this project were to establish a stratified sample of snags across the Willamette National Forest to be repeatedly sampled over time and to elucidate factors that are associated with the use of snags by wildlife (primarily bird) species.

In this report, we provide summary statistics of 1,267 snags (96 percent were artificially created, 4 percent natural) that we monitored during 1997 and 1998. In addition, we report the results from statistical analyses that addressed the question: Was total woodpecker use of created snags associated with structural characteristics of the snag and the stand?

Methods

Study Area

The study occurred on the Willamette National Forest (WNF) in Marion, Linn, and Lane counties, Oregon in west central Oregon in the Cascade Mountains.

Criteria for Selecting Stands with Created Snags

We surveyed a sample of stands that was stratified by elevation, year of snag creation, and WNF Ranger District. The initial pool of stands subsampled was developed using the WNF's stand treatment database (STD). This database contains details on all management activities for each stand on the WNF. We first queried STD for all stands containing created snags. Because we intended to collect data on every created snag within a stand, we chose stands that contained only as many snags as we thought we could survey during one working day (40 or less). We therefore shortened the initial list by selecting only those stands that contained from 10-40 created snags.

From this shortened list, we stratified the sample by median elevation (915 m), median year of snag creation (1993), and seven WNF ranger districts to obtain a diversity of tree species, wildlife using the trees, and tree decay levels (obtained from sampling trees killed in different years). In one of the WNF's Ranger Districts

(Lowell), there were no stands above 915 m that met our criteria. We used the median values as breaking-points and randomly sorted all the stands from the shortened list into the appropriate categories, and then randomly selected stands within each cell using Microsoft Excel's random number generator *(table 1)*.[4] For each of the randomly selected stands, we intended to locate and monitor all of the created (but not natural) snags in the stand, but this did not always occur.

Table 1—*The initial sampling regime for the study. For each of the cells shown in this table, four stands were randomly selected from the entire list of stands in the WNF's STD that contained from 10-40 created snags. In the Lowell Ranger District, there were no stands above 915 m that met these criteria, so two of the cells (denoted by "NA" in the table) in the sampling regime were empty. There were a total of 55 stands sampled. These were evenly distributed between each of the Ranger Districts, elevations, and age classes.*

	Elevation ≤ 3,000 feet		**Elevation > 3,000 feet**	
Ranger District	**Snag created ≤ 1993**	**Snag created > 1993**	**Snag created ≤ 1993**	**Snag created > 1993**
Detroit				
Sweet Home				
McKenzie				
Blue River				
Rigdon				
Oakridge				
Lowell			N/A	N/A

Logistical Problems Altered the Sampling Design

The trees that we selected for snag creation did not represent an unbiased, random sample of trees with or without prior wildlife use because of three major problems:

- Problem 1—Inaccessibility: Several of the stands that were selected at random were not accessible due to road closures (e.g., from mudslides or extensive tree fall-down over roads). When these road closures occurred > 1 mile from our randomly selected stand, we omitted the stand from the study. When this occurred, we substituted the nearest accessible stand in the same cell in our sampling design as the omitted stand.
- Problem 2—Stands without created snags: All of the stands that were selected at random were reported, in the stand treatment database (STD) to contain between 10-40 created snags. However, when we arrived at several of the stands, we were unable to locate any created snags. When this occurred, we substituted the nearest accessible stand in the same cell in our sampling design *(table 1)* as the omitted stand.
- Problem 3—Stands with more than 40 created snags: A third problem we encountered was that the actual number of created snags in a stand far exceeded the number reported in the STD. When we encountered stands with

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> 40 created snags, we arbitrarily chose a starting point within the stand (usually near the landing) and sampled the first 40 trees that we encountered.

Finally, in addition to the stands that we selected and surveyed for the first time, we also re-surveyed 311 natural and artificially created snags that had been monitored in 1995 following a nonrandom selection process (Shope 1995).

Features of Created Snags That Were Recorded

We marked each created snag with a unique number on two aluminum tags (to facilitate relocating the snag in the future) and recorded its position (latitude, longitude, and elevation) with 1-m accuracy using a global positioning system (Trimble Pathfinder Pro XL) with differential correction (Trimble Pathfinder Office, version 1.1). We also recorded all the features at each created snag *(table 2)* and a stand level variable called "lscape" that we created.

Table 2—*Description of features recorded at each created snag.*

Snag Feature	Units	Methods
Species	Species code	Visual assessment of snag species
Year killed	Year	Year snag created. Obtained from Stand Treatment Database at the Willamette National Forest Supervisors Office, Eugene, Oregon
DBH	Inches	Used a diameter tape to measure diameter at breast height of snag.
Height	Feet	Used a clinometer and rangefinder to measure current height of snag.
Decay class	1, 2, 3	Visual estimation of decay class (Parks and others 1997).
Elevation	Meters	Obtained from GIS coverage listing the mean elevation of all harvested stands on the WNF
Pct bark	0-100 pct	Visual assessment
Status	Live or dead	Live snag was one with at least one branch with green needles Dead snag was one with no branches with green needles
# limbs	Count	Visual assessment of # dead and live limbs > 0.91 m long that extend from bole
# green branches	Count	Visual assessment of # green limbs. Green limbs are limbs that have at least one green leaf.
Treatment	Natural, sawed, blasted, inoculated, girdled, unknown, other	Visual assessment
Damage type	Lightning, conch, logging, insect, list others	Visual assessment for lightning scars, fungal conchs, logging damage, insect damage, wind damage, etc.
Pct damage	0-100 pct	Visual assessment of percentage of tree with specific damage types.
Fire scar	Yes, No	Visual assessment of fire scars.

Snag Feature	Units	Methods
Pct fire scar	0-100 pct	Visual assessment.
Sapsucker use	Yes, No	Visual observation of linear rows of small holes in trunk or limbs (Bent 1964).
New pileated foraging excavations	Count	Count of rectangular-shaped, approximately 5 cm deep and lighter in color than the surrounding wood, or with fresh wood shavings at the base (Bent 1964).
Old pileated foraging excavations	Count	Count of rectangular-shaped, approximately 5 cm deep and the same color as the surrounding wood (Bent 1964).
New woodpecker foraging excavations	Count	Count of foraging excavations that are not rectangular in shape, approximately 5 cm deep, lighter in color than the surrounding wood, or with fresh wood shavings at base, but are not rows of small holes.
Old woodpecker foraging excavations	Count	Count of foraging excavations that are not rectangular in shape, approximately 5 cm deep, same color as the surrounding wood, but are not rows of small holes.
New nest cavities	Count	Count of foraging excavations that appear very round or elliptical in shape and appear to be hollow in the interior. Also, the foraging excavation appears to a lighter color than the surrounding wood and/or fresh wood shavings at the base.
Old nest cavities	Count	Count of foraging excavations that appear very round or elliptical in shape and appear to be hollow in the interior. Also, the foraging excavation appears to the same color as the surrounding wood.
Other use	Yes, No	Visual assessment of other wildlife use. For example, bear scratches or current use by a chipmunk, squirrel, or bird. Record in notes.

We classified foraging excavations (holes in the bark, not scalings) and nest/roost cavities in the created snags as new or old. New foraging excavations and cavities were those that were a lighter color than the surrounding wood and/or had fresh wood shavings at the base. Old foraging excavations and cavities were the same color as the surrounding wood and did not have fresh wood shavings at the base. The new foraging excavations were potentially the more reliable observations for addressing use of created snags because they were obviously done after the snag was created. Although old use may have occurred after snag creation, it may also have been present before the snag was created. Hereafter, foraging excavations and nest cavities in the created snags will be referred to as new or old.

Pileated woodpecker *(Dryocopus pileatus)* foraging excavations were distinguished from all other types of foraging excavations by their rectangular shape and depth between 3 cm and 1 m deep (Bent 1964). Sapsucker foraging excavations were not classified as new or old but were distinguished from all other foraging excavations by their unique pattern of deeply cut holes, less than 0.5 cm in diameter and usually arranged in horizontal lines around the trunk (Bent 1964). Nest or roost cavities were distinguished from foraging excavations by their round or elliptical shape typical of certain woodpecker species such as pileated woodpecker and Northern flicker *(Colaptes auratus),* which were common in the study area.

Creation of Landscape Variable

We used geographic information systems (GIS) to create a stand level variable for the regression analyses called "lscape": the amount of late-successional forest in the adjacent landscape (i.e., within 500 m of the stand). Below we briefly outline the series of steps taken in GIS to create this variable.

The "lscape" variable was created by first identifying the predominant size-class of the trees within 500 m of each stand of created snags using ARC INFO, GIS software. We then calculated the percent of area in each stand's 500 m buffer that consisted of size classes typical of late successional forest on WNF. The size classes in the Veg6 GIS data layer that most closely fit this criterion are codes 6.0 through 7.1, which correspond to large (83-121 cm dbh) and giant (> 121 cm dbh) trees. In addition, the Veg6 data layer contains one size-class category (class 5.5) that includes both medium (53-82 cm dbh) and large trees. For the purposes of this analysis, we class 5.5 to be large trees.

Analyses

Descriptive Statistics

We calculated descriptive statistics using Microsoft Excel.

Regression Analyses

We used logistic regression to analyze the relationship of woodpecker use of created snags associated with snag and stand characteristics using S-Plus software version 4.5 from MathSoft, Inc. The presence or absence of new woodpecker foraging excavations on a created snag was the response variable in the models, and the variables listed in *table 2*, along with Universal Transverse Mercators, "lscape," and elevation, were the explanatory variables representing snag and stand characteristics.

The regression models were constructed using two data sets, one with 1,267 snags (96 percent created snags) excluding the explanatory variable, "snag age" (years since tree killed), and another with 1,223 records that included the explanatory variable "snag age." Two data sets were used because snag age was an additional characteristic that might have to be associated with bird use. The different sample size in each data set was due to some missing data on the year of snag creation for certain stands.

Results, Discussion, and Recommendations

Descriptive Statistics

Types of Snags Monitored

We monitored 1,267 snags in 55 harvested stands on seven districts of the Willamette National Forest over 1997 and 1998. The elevation of the created snags ranged from approximately 333 m to 1,848 m. Approximately 85 percent of the snags were artificially created by blasting or saw topping, 11 percent by girdling or inoculating, while 4 percent were natural. The blasted and sawtopped snags were all over 27 m in height. The blasted snags ranged in dbh from 38 to 191 cm; the saw-top snags ranged from 40 to 183 cm dbh; the one girdled tree was 62 cm dbh; and the natural snags ranged from 53-172 cm. Eighty-seven percent were Douglas-fir *(Pseudotsuga menziesii),* 38 percent were still partially alive with green branches, and 95 percent were in the first two stages of decay (decay classes follow Parks and others [1997] in which class 1 represents those trees that died recently and retain most of their bark and branches with their top intact; class 2 represents those snags that have been dead at least several years and have lost some branches and some bark; and class 3 represents those snags dead a long time and lack branches and bark).

We report only new bird use below because we cannot be certain that old bird use was not done before the snag was created.

- Foraging use by sapsuckers and pileated woodpeckers: Only 1.5 percent of the snags had new foraging excavations by pileated woodpeckers. Sapsucker use was present on 1.5 percent of the snags.
- Foraging use by other birds: Nearly half of the created snags monitored (49 percent) had new foraging excavations from other woodpeckers and other unidentified excavators.
- Nest/Roost cavities in created snags: New cavities were present on 1.2 percent of the snags. Of the 17 snags with new cavities, 2 were naturally created; 1 was girdled; 1 was unknown; and the rest were blasted or saw-topped. Also, of these 17, 2 had class 1 decay, 2 were class 3 decayed, and the rest were class 2 decay. The majority of these 17 snags had 80 percent of their bark remaining with 7 having 60 percent of their bark remaining.
- Use by species other than birds: Evidence of use by species other than birds on the created snags was present on 1.8 percent of the snags. Detecting use by other species was difficult since they did not always leave obvious signs. However, we did observe an unidentified species of bat leaving one created snag and a chipmunk climbing up another.

There were few created snags in this project with foraging use by pileated woodpeckers and sapsuckers. The majority of created snags that we monitored were recently killed (within the last 10 years), had little decay, and therefore, may not house carpenter ant colonies, one of the major prey items of the pileated woodpecker (Bent 1964). The low level of use by these species could also reflect their limited abundance in the forests surrounding the harvested stands we surveyed. We did not conduct bird abundance studies in the harvested stands that we monitored.

Nearly half of the created snags had new foraging excavations by woodpeckers and other unidentified excavators, indicating that one or more species that occur in the elevation range of our project (e.g., hairy woodpecker *[Picoides villosus],* downy woodpecker *[Picoides pubescens],* or red-breasted nuthatch *[Sitta canadensis])* were using these snags for foraging.

There were few created snags in this project with nesting or roosting cavities. The majority of created snags that we monitored had little decay and therefore may not have been soft enough for cavity foraging excavation by some birds. The low level of cavities could also reflect the limited abundance of cavity excavators in the forests surrounding the harvested stands we surveyed.

Bird Use Associated with Created Snag and Stand Characteristics

New Woodpecker Foraging Excavations

We conducted regression analyses to investigate whether new woodpecker foraging excavations were associated with snag and stand characteristics. This analysis was based on the null hypothesis that new woodpecker foraging excavations were random events.

The data set used in the analysis contained 1,267 created snags with the response variable presence/absence of "new woodpecker foraging excavations" and the explanatory variables listed in *table 2* (excluding snag age). Data was analyzed using the following steps:

- First**,** presence/absence of new woodpecker foraging excavations was statistically tested against all explanatory variables using logistic regression for binary responses. Stand differences were found to be statistically different. Stand-level variables, such as "lscape" and elevation, were not found to be significantly associated with stand differences in the response variable.
- Next, the same logistic regression model was rerun with the 1,267 snags and this time corrected for stand differences. This means that, within the regression model, the stand average count (total count in that stand divided by the number of created snags in that stand) was subtracted from each individual snag count. This put all of the snags on an even basis, as if they all were from the same stand. Obviously, this eliminated all stand-level differences. We did this only after checking all stand-level variables for significance (and finding none), and only when "stand," as a categorical variable, was significant.

This second model provided convincing evidence that the status (live or dead) of the created snag was associated with the presence/absence of new woodpecker foraging excavations (p-value <0.00004). Specifically, the odds of the presence of new woodpecker foraging excavations on dead created snags was estimated to be 2.3 times the odds of the presence of new woodpecker foraging excavations on created snags that were still living (95 percent Confidence interval: 1.5 times to 3.4 times) *(table 3).* Many of the foraging excavations were deep (greater than 5 cm) into the cambium, where the woodpeckers may have been foraging for insects. Insect colonies may be more abundant in dead trees than in live. This inference may be useful in selecting a preferred method of snag creation and/or post-creation treatments.

We did not randomly select which trees within each of the harvested stands were to be converted to snags, therefore this project was observational. Stronger inferences about the association of bird use with created snag characteristics may be gained by instituting experimental controls in future snag creation efforts.

Table 3—*Coefficients and equation for the logistic regression model providing convincing evidence that the status (live or dead) of the created snag and the presence of old woodpecker foraging excavations were associated with the presence/absence of new woodpecker foraging excavations (p-value <0.00004).*

Equation: $\log\left(\frac{\pi}{1-\pi}\right) = \beta_0 + \sum_{i=1}^{55}\left(\beta_i s \tan d_i\right) + \beta_1 + \varepsilon$ where π is the proportion of new woodpecker foraging excavations, "stand$_i$" is an indicator variable for each stand (correcting for between stand differences), β_1 is a binary, categorical variable with a value of 0 if the created snag is dead and a value of 1 if the created snag is still alive, and ε is error. The sample size is 1,267 created snags, null deviance is 1,736.93 on 1,266 degrees of freedom, and residual deviance is 1,141.67 on 1,211 degrees of freedom.

Coefficient	Interpretation of coefficient	Standard error	p-value
β_0 0.458401	Intercept	0.874047	0.60000
β_1 -0.82203	Categorical variable 0=dead created snag 1=live created snag	0.197628	0.00003

Future Monitoring

The created snags in this project should be monitored over several years to observe current bird foraging and nesting during the spring breeding season when the actual birds, rather than just their foraging sign, can be documented. This could provide evidence on which species were not using these snags in the harvested stands, as well as information on what density and placement of created snags was associated with more frequent bird use. This may provide evidence that species such as the red-breasted nuthatch, identified as the primary cavity excavator and upon which several Willamette National Forest post-harvest snag retention rules are based (USDA Forest Service 1994), were utilizing the snags for nesting or roosting. Also, more studies should be initiated to monitor wildlife use of created snags before and after the snag is killed and in subsequent years. Wildlife use could also be compared between blasted, sawed and fungus and insect inoculated snags to learn more about the effect of each of these kill methods on wildlife use. Features monitored at each created snags should include insect use, because insects attract birds and other wildlife. In addition, fall down rates should be monitored as the snags age. This information will assist Willamette National Forest land managers with compliance with the Pacific Northwest Regional Forest Planning regulations (USDA Forest Service 1990, 1994) regarding selection and monitoring of snags left in harvested stands.

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The Efficacy of Inoculating Fungi into Conifer Trees to Promote Cavity Excavation by Woodpeckers in Managed Forests in Western Washington[1]

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Abstract

To develop management prescriptions to promote the use of forests by cavity-using wildlife, we have investigated the relationship that wood-decay fungi play in facilitating nest excavation by woodpeckers. We located 78 woodpecker nests in western Washington and documented the presence of basidiocarps and collected wood samples to identify the decay organisms in trees. Basidiocarps of *Fomitopsis pinicola* (red-belted conk) were found on 47.4 percent of all woodpecker nest trees. This fungus was also recovered from wood samples of 7.7 percent of all woodpecker nest trees that did not possess conks. We also identified 32 other fungal types from 20 genera in woodpecker nest trees. We selected *F. pinicola* as the organism to inoculate into trees experimentally to promote colonization by woodpeckers, because this was the most common fungus associated with woodpecker trees and because it met several other criteria. In 1997 and 1998, we inoculated 65 clusters of 10 trees in 34 separate managed forest stands in western Washington. The experimental design of inoculations will allow us to examine the effect of blank (control) vs. fungal inoculations, the influence of tree species (i.e., *Tsuga heterophylla, Pseudotsuga menziesii*), the effect of available snags, and the effect of size/age classes of trees on future colonization by woodpeckers. Visual examinations for presence of mycelia and/or conks, and retrieval of wood samples and isolation of fungal cultures from randomly selected trees (*N*=58) inoculated in 1997 and 1998, indicated the successful colonization of *F. pinicola* in 50 percent to 70 percent of the trees inspected in 1998 and 1999.

Introduction

Most, if not all, cavity-using wildlife are dependent on woodpeckers (e.g., *Picoides* spp.) that excavate cavities (Jackman 1975, McClelland 1977). In western Washington, for example, at least 54 species of birds and mammals require or use tree cavities excavated by woodpeckers (Brown 1985). However, woodpeckers mostly excavate cavities in trees that have decay caused by certain types of

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filamentous fungi, primarily basidiomycetes, that soften the wood of living, injured, and dead trees (Bull and others 1997). Therefore, the interaction between fungi and woodpeckers represents a keystone process that may be necessary to support a robust diversity of wildlife and to complete the complement of vital processes necessary for healthy forest ecosystems.

Traditionally, cavity-using wildlife have been associated with old-growth forests and researchers have suggested or implied that old forests were needed to support these species (e.g., Conner and others 1994). However, because cavities are correlated with old-growth forest, it is not known whether some species of wildlife require mature forests *per se*, or just require a suitable incidence of cavities or snags. The overall objective of this study is to facilitate creation of cavities for wildlife in trees of managed forests in western Washington (see Huss and others 1999).

Specific objectives of this article are to describe the species of fungi associated with woodpecker nest cavities, report on our selection of a fungal species for inoculation into trees to promote use by woodpeckers, describe the protocol for inoculation of a potentially-beneficial fungus into managed forests, and determine the efficacy of treatment for the establishment of fungi.

Materials and Methods

Woodpecker Nest Surveys

During woodpecker nest searches in 1996-1997 we established four general study areas: (1) North Forks, (2) West Forks, (3) Hoh Valley, and (4) Blue Mountain (*fig. 1*, Bednarz and others 1997). In 1998, we searched for woodpecker nests mostly in selected areas in the North Forks and West Forks study areas. The North Forks area was located 6 km north and 11 km west of Forks, Washington, in Clallam County. The West Forks area was relatively small in size (approximately 31 km^2) and was located about 11 km west of Forks, Washington (Clallam County). The Hoh Valley area was approximately 78 km^2 in size and was about 32 km east and 16 km south of the town of Forks, Washington (Jefferson County). The Blue Mountain area covered roughly 93 km^2 and was located approximately 13 km west and 8 km south of Oakville, Washington (Pacific County). The three Forks study sites were primarily dominated by western hemlock *(Tsuga heterophylla)* with secondary dominant tree species consisting of Douglas-fir *(Pseudotsuga menziesii)* and Sitka spruce *(Picea sitchensis).* Douglas-fir and western hemlock were codominant in the Blue Mountain study area. We incidentally collected data at some woodpecker nests located outside of the described study areas, but these were in ecologically similar environments. All study areas were comprised of state or private lands managed primarily for timber production. Forest habitats consisted of a mosaic of different even-aged forest stands ranging from recently clearcut areas to stands more than 100 yr old. Stands surveyed were generally small, ranging from 10-160 ha in size, and were often bordered by stands which had been clearcut within the last 5 yr.

We conducted nest searches by walking through stands and searching either for woodpeckers or for large snags or partially dead trees with fresh cavities. Fresh cavities were recognized by the presence of recent wood shavings near the base of trees or by recently-exposed wood around the perimeter of the cavity entrance. When a fresh cavity entrance was found, we stayed in the vicinity and watched for woodpecker activity for 30-60 min. In addition, if woodpeckers were detected during a search, we attempted to follow them to their cavities.

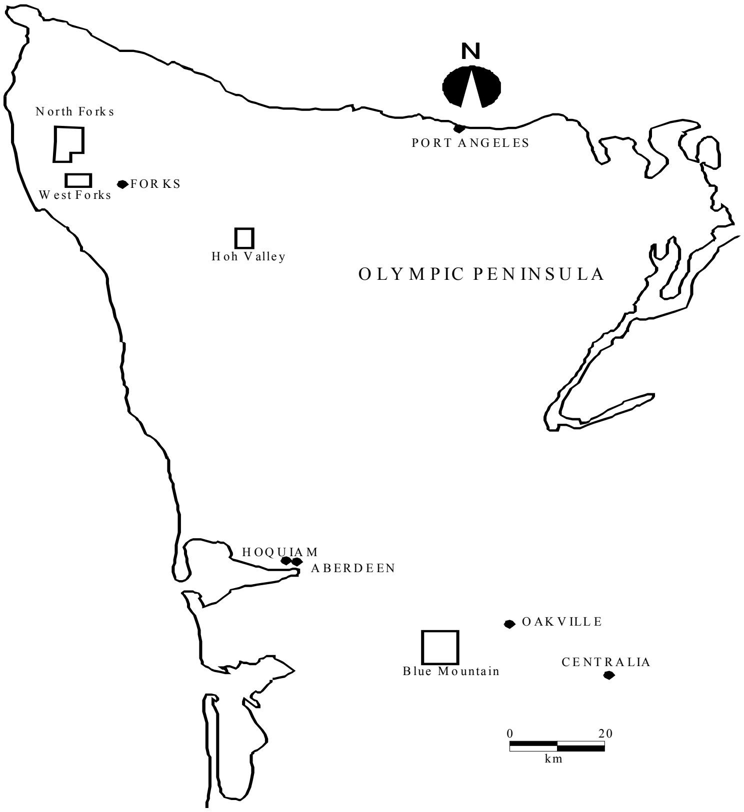

Figure 1—Location of study areas in western Washington. Square and rectangular symbols indicate specific study sites.

Collection of Fungi Associated with Nest Trees

The presence or absence of fungal reproductive bodies or basidiocarps (e.g., conks, bracket fungi) were noted for each nest tree or nest snag. When present, several samples nearest to the cavity entrance were collected. In most cases, we climbed the tree to collect samples. However, when it was unsafe to climb the snag, samples of wood were taken as close as possible to the opening of the nest cavity and conks were retrieved by knocking them off the tree with a pole.

Basidiocarps were air-dried at room temperature to help preserve their appearance and to inhibit degradation. Specimens were stored with Revenge Bug Strips® (Roxide International, Inc., New Rochelle, NY)[5] to prevent pest infestations. Fungal species were identified based on micro- and macroscopic features using standard identification keys (e.g., Arora 1986, Miller 1972, Overholts 1953, Smith and others 1981). Basidiocarps were also examined by Robert L. Gilbertson

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[5] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

(University of Arizona) and N. Jay Justice (Arkansas Department of Environmental Quality) to confirm species identification.

Aging of Basidiocarps

Air-dried basidiocarps were weighed to determine their mass and then aged. Many members of the Order Aphyllophorales develop perennial basidiocarps that add a new layer of pores (i.e., spore-producing regions) each year (Alexopoulos and others 1996, Moore-Landecker 1996). The age of the basidiocarp can be determined by counting the number of pore layers established before the actively-growing leading front (1 ridge = 1 yr). In specimens where these outer ridges were less distinct, the basidiocarp was cut longitudinally using a saw. The inner surface was then planed using a scalpel blade so that the number of pore layers could be counted more readily. The age of these perennial basidiocarps indicates when the conk began to form on the surface of the tree, and provides a minimum estimate for how long the fungus was growing on the tree.

Isolation of Fungal Cultures from Basidiocarps

Tissue from the edge of each basidiocarp was removed using a pair of needle-nosed pliers and stored temporarily in a sterile petri dish. After sterilizing with pressurized steam in an autoclave, 20-25 ml of isolation medium (one of two types; Isolation medium #1 and #2; see Bednarz and others 1997) was poured into sterile 100 x 15 mm petri dishes. After the medium had solidified (due to the presence of agar in the culture medium) and cooled, a single fragment of the tissue sample was transferred to the center of the plate using a sterile forceps. These isolation media were nutritionally weak and contained substances to inhibit the growth of fast-growing and potentially contaminating microorganisms while selectively encouraging the growth of a fungal culture from basidiocarp tissue (Tsao 1970). All plates were incubated at room temperature (~24 °C) and checked periodically for the presence of filamentous growth.

Fungi Associated with Wood Samples from Nest Trees

Collection of Wood Samples

Wood samples obtained during the 1996 field season were collected from above, below, and to the right and left sides of the woodpecker cavities and/or at the base of nest trees. Collection of wood samples during the 1997 and 1998 field season was restricted to one or two wood samples obtained directly below the nest cavity and/or at the base of the nest tree. In cases where the wood was less decayed and sound, the sample was removed with an increment borer (5.15 mm diameter). In cases where the wood was too soft to remove with the increment borer, we employed a portable rechargeable electric drill with an 8.00 mm diameter auger drill bit. A hole was drilled 10-15 cm into the tree and particles of wood were collected into sterile plastic collecting bags as the drill bit was withdrawn. Samples were kept refrigerated until we could isolate resident fungi from the wood.

Isolation of Fungi from Wood Samples

Fungi isolated from wood samples collected in 1996 followed the protocol given in Bednarz and others (1997). Culture isolation medium #3 (Bednarz and others 1997) was employed for isolation of fungi from wood samples collected in 1997 and 1998. This medium consisted of a mixture of 20 g of dehydrated malt extract broth, 20 g of agar, 0.2 g of pentachloronitrobenzene (PCNB), and 1 liter of distilled or deionized water. The medium was sterilized by autoclaving at 15 psi at 121°C for 15 min. After cooling to 50-60°C, 2 ml of a filter-sterilized antibiotic stock solution (20,000 units/ml of penicillin and 80,000 units/ml of streptomycin in distilled water) and 1 ml of a benomyl solution (0.1 percent benomyl in 100 percent ethanol) were incorporated into the medium.

Identification of Fungal Cultures

For filamentous fungi and some yeasts, identifications were based on the morphology of cultures growing on malt extract agar and on microscopic characteristics (e.g., reproductive structures, spore morphology, or formation of hyphae). Slide cultures for viewing under the microscope (Larone 1995) were produced by allowing inoculum of the fungal culture to grow on a block of malt extract agar sandwiched between a microscope slide and glass coverslip. Cultures were placed in a moist chamber to prevent the medium from drying out and were incubated at room temperature (24 °C) for several days. After the fungus had grown to the edges of the culture medium onto the surface of the slide and/or glass coverslip, the block was removed and the coverslip transferred to a fresh microscope slide to which a drop of lactophenol with cotton blue dye (Larone 1995) had been added. When enough growth was present, a second slide was prepared by adding a drop of the same mounting medium to the surface of the slide and placing a fresh coverslip over it. The edges of the coverslips were sealed with clear fingernail polish to produce semi-permanent slides.

A variety of literature sources and identification keys were consulted to identify all fungal specimens and cultures to provide some taxonomic category (Arora 1986, Barnett and Hunter 1998, Larone 1995, Miller 1972, Nobles 1948, Overholts 1953, Rayner and Boddy 1988, Rippon 1988, Smith and others 1981, Taylor 1974). Many of the cultures isolated from wood samples were unicellular yeasts. Yeast species are not readily identified based on microscopic characteristics; however, yeasts can be sorted, sometimes to species, based on the outcome of certain physiological tests (e.g., assimilation of various types of sugars). Yeast cultures were tested based on the analytical profile index (API) system for diagnosis of yeasts (diagnostic kits, bioMérieux Viteck, Inc., Hazelwood, MO). We consulted the API data base and identified as many of the yeast species as close to the species level as possible.

Field Inoculations

Selection of Inoculation Sites

We developed an experimental design *(table 1)* to test the effects of tree species, available snags, and size/age classes of trees on the resulting use of inoculated trees by woodpeckers *(table 1)*. This experiment was set up in a hierarchical fashion so we should be able to examine these effects independently and the interaction of these factors. This evaluation will be done during the next stage of the study to be implemented in 3-10 yr.

Table 1—*Original experimental design for inoculation experiments of Douglas-fir* (Pseudotsuga menziesii) *and western hemlock* (Tsuga heterophylla) *trees.*

Treatments	**Presence of snags**[1]	**Age/size class of trees**[2]	**Number of clusters**	**Number of trees per cluster**
Control Group	Snags absent	Old	4	10
		Young	4	10
	Snags present	Old	4	10
		Young	4	10
Treatment Group	Snags absent	Old	4	10
		Young	4	10
	Snags present	Old	4	10
		Young	4	10
Total:	2 tree species X 64 clusters X 10 trees/cluster = 640 trees			

[1] Snags absent = < 7 snags (>50 cm dbh)/ha; Snags present = > 7 snags/ha.

[2] Age class designation; young = approximately 50 years old, 30-45 cm dbh; old = approximately 70 years old, 40-60 cm dbh.

Selection of field sites was done with the cooperation of land owners. During this process, we worked closely with representatives from Rayonier, the Washington Department of Natural Resources (DNR), Weyerhaeuser, Port Blakely Tree Farms L. P., I. P. Pacific Timberland Inc., and Hancock Timber Resource Group. Candidate stands for inoculation were required to satisfy the following criteria: supported western hemlock or Douglas-fir as a dominant or co-dominant species and included trees that could be classified as either: (1) relatively small-diameter (<40 cm dbh)/relatively young (approximately 30-50-yr-old trees), or (2) relatively large-diameter (> 40 cm)/relatively old (> 60 yr) stand. We further classified stands into one of two snag-status categories: (1) snags conspicuously present (about 7 per ha), or (2) large snags mostly absent.

In most cases, inoculated and control clusters (each including 10 trees) were located in the same forest stand. In some cases, stands were either not large enough to accommodate two clusters of experimental trees or the structure varied within the stand. In these cases, we located the control cluster in a nearby stand. When experimental and control clusters were placed in separate stands, we made an effort to use stands of similar characteristics (e.g., same dominant tree species, age, and snag density).

Fungi Used in Field Inoculations

Because of the high incidence of *Fomitopsis pinicola* observed associated with woodpecker nest trees during the 1996 field season and its benign nature as a cause of brown rot in wood (e.g., brown-rotter: capable of utilizing primarily cellulose and hemicellulose in wood but not lignin [Rayner and Boddy 1998]), we chose this organism in our field tests. Three basidiocarps of *F. pinicola,* from three different study locations in western Washington were used to derive mycelial cultures (Bednarz and others 1997). Cultures of these individuals were morphologically indistinguishable from one another, but vegetative compatibility analysis (Huss 1993, Mounce 1929, Worrall 1997) of the these isolates indicated that these represented three genetically-distinct individuals of *F. pinicola* (*i.e.,* basidiocarps no. 36 and 64 from hairy woodpecker *[Picoides villosus]* nests 17 and 36, respectively, and basidiocarp no. 43 from northern flicker *[Colaptes auratus]* nest 22).

Preparation of Wooden Dowel Spawn

Dowel plugs (12.8 cm long) were cut from 2.24 cm diameter hardwood. A 0.96 cm diameter hole was drilled down the center of each dowel using an auger drill bit to create an axial channel (C. G. Parks, pers. comm.). Plugs were soaked in distilled water (1:4 mass to volume - 1 kg of wood per 4 l of water) for 12 hr. Plugs and water were autoclaved (i.e., 121°C at 20 psi) for 30 min. The contents were allowed to cool and were soaked overnight. Excess liquid was decanted off the dowel plugs followed by a rinsing with distilled water. Dowels to be used for the control inoculations were prepared in the same manner but autoclaved a second time for 1.5 hr to insure that any resident microorganisms were killed.

A sterilized grain medium was used in conjunction with dowel plugs to support good mycelial growth and reduce the time necessary for the fungus to invade the wooden substrate. Dry millet and perlite (4:1 by weight) were mixed together, then added to distilled water in a ratio of 1 part by weight of dry ingredients to 1.5 parts by volume of distilled water (i.e., 1 kg of grain/perlite for every 1.5 liters of distilled water). This mixture was autoclaved (i.e., 121°C at 20 psi) for 30 min, then allowed to cool to room temperature and any excess liquid was drained off. Gypsum (2 percent by weight of $CaSO_4 \bullet 2H_2O$) and powdered chalk or whiting (0.5 percent by weight of $CaCO_3$) were mixed into the cooked grain medium to help buffer the pH and to help prevent the grain from sticking together (Elliot 1985, Fritsche 1978).

Plugs were loaded with grain medium by stuffing material into their axial channels. Twenty-five wooden dowels were placed into a square aluminum cake pan (20.3 x 20.3 x 3.7 cm) and 250 ml of malt extract broth was poured over the surface of these dowels. The surfaces of the dowels were lightly covered with grain/perlite medium. The pan was placed into an autoclavable spawn bag with filter patch (Dimensions: 53.3 x 20.3 x 12.1 cm, Fungi Perfecti, Olympia WA) and the end of the bag was sealed with wooden clothes pins. The bag and its contents were autoclaved for 1.5 hr, then allowed to cool. After sterilization the dowels were inoculated with mycelium of *Fomitopsis pinicola* (isolates 36A or 64A) that had been grown previously on 2 percent malt extract agar. Material was incubated at room temperature for 2-3 mo. and growth was monitored.

Inoculation of Control and Test Stands of Trees

Inoculations of trees were made by climbing approximately 8 m (within one standard deviation of the mean height of woodpecker nests) up a Douglas-fir or western hemlock tree and a 2.24 cm to 2.56 cm diameter hole was drilled, 5-8 cm deep using an battery-operated drill. A manually-operated brace was then used to drill out the remaining hole to a depth of 13-15 cm. A blank or inoculated dowel was inserted into the hole and a piece of PVC tubing (7.70 cm long by 2.56 cm in diameter) was inserted in the hole adjacent to the dowel. About 5 cm of the tubing remained outside the entrance of the hole to prevent the tree from healing over this wound (C. G. Parks, pers. comm.). Holes were made on the north sides of trees, which was where woodpeckers most often excavated their nests (Bednarz and others 1998). Fungal inoculations were made using dowels impregnated with cultures 36A and 64A of *F. pinicola*.

A subset of the trees were inoculated with culture 64A in a similar manner as described above but using dowels of a smaller diameter (1.0 cm and 1.4 cm) with no axial channels drilled through the center. Holes drilled for these dowels were 1.28 cm to 1.60 cm in diameter. After the blank or inoculated dowel (7.7 cm long piece 1.28 cm diameter) was inserted into the hole, PVC tubing was driven 2.56 cm into the hole with a rubber mallet.

Inspection and Sampling of Trees Inoculated in 1997 and 1998

All experimental tree stands that we established in 1997 were visually inspected in 1998 and 1999 to determine if there were any signs of fungal establishment or other changes. In 1998, we randomly selected 10 clusters treated with viable inoculum and collected wood samples from two trees (a total of 20 trees) in each cluster to determine if *F. pinicola* isolates 36A or 64A were established. In 1999, we randomly selected 19 clusters and collected wood samples from two trees per cluster (20 trees inoculated in 1997 and 18 trees inoculated in 1998). Wood cores were extracted from trees using an increment borer (5.15 mm diameter), about 1 cm below the inoculation hole and extending 5-10 cm into the tree. Prior to use on each tree, the increment borer was rinsed in 70 percent isopropyl alcohol to sterilize the surface. Wood cores were placed in sterile plastic bags and kept refrigerated until isolation of fungi could be accomplished. Tree wounds were covered with a pruning sealant to minimize exposure to other fungi.

Isolation of *Fomitopsis pinicola* from Wood Samples

Four isolation plates per wood sample were established using isolation medium #3. Bits or particles of wood were transferred, using a sterile forceps, to the center of a 100 x 15 mm petri dish containing 20-25 ml of the isolation medium. All isolation plates were incubated at room temperature (24 °C) and checked periodically for the presence of fungal growth. After colonies appeared on the plate, a piece was transferred and grown on culture plates containing a 2 percent malt extract agar and incubated at room temperature for a 1-2 weeks. Culture and microscopic characteristics were checked to determine whether the fungus was *F. pinicola* or some other fungal species. Isolation procedures were repeated for wood samples that did not yield this fungus to determine its presence or absence in the collected wood samples.

Vegetative Compatibility Analysis

Isolates of *F. pinicola* were paired with stock cultures of *F. pinicola* (36A, 43A, and 64A) on malt extract agar plates and incubated at room temperature for several weeks. The plates were examined for lines of demarcation that are indicative of vegetative incompatibility and suggest when isolates are genetically different. If no lines of demarcation were observed between the two paired colonies then this would suggest that isolates represented the same genetic individual. This test was employed to determine if the cultures inoculated into trees represented the same fungus extracted from the tree (Bednarz and others 1997, Huss 1993).

Results and Discussion

Woodpecker Nests

Between 1996 and 1998, we located and collected data from 78 cavities occupied by nesting woodpeckers on or near the study areas *(fig. 1)*. These included 51 hairy woodpecker cavities, 26 northern flicker cavities, and 1 red-breasted sapsucker cavity. We saw and/or heard pileated woodpeckers occasionally but these birds were extremely wide ranging and we did not document nesting. In 1997, we observed a single downy woodpecker in the Blue Mountain study area, but could not locate its nest. While we did occasionally detect red-breasted sapsuckers in the Forks area, nesting activity was only recorded in the Blue Mountain study area *(fig. 1)*.

Fungal Diversity Based on Basidiocarp Data (1996-1998)

Fungal basidiocarps were present on 50.0 percent of the woodpecker nest trees (N = 78). Of the 82 conks collected over the course of 3 yr, 93.9 percent represented *Fomitopsis pinicola* (mean age = 7.9 yr; mean mass = 221.6 g), 2.4 percent represented *Ganoderma applanatum* (mean age = 8.5 yr old; mean mass = 105.8 g), and 3.7 percent represented *Trichaptum fuscoviolaceum* (mean age = 1.3 yr; mean mass = 2.4 g). Among hairy woodpecker nest cavities for 1996-1998, evidence of fungal basidiocarps was present on 54.9 percent of all trees regardless of tree species (N = 51). Basidiocarps were found on 42.3 percent of the northern flicker nest trees (N = 26). The mass and age of the conks from *Fomitopsis* and *Ganoderma* indicate that these fungi were growing in the wood for a substantial period of time before excavation of the tree by woodpeckers. These organisms are completely heterotrophic and obtain all their nourishment from the wood they decay. Consequently, inoculation of trees intended for the purpose of attracting woodpecker and other cavity utilizing species will likely take a minimum of 5-10 yr before colonization occurs.

Wood Samples and Culture Isolations

Of the 211 wood samples collected from nest trees during the summer field seasons of 1996-1998, at least 33 different fungal types representing 21 genera were isolated and identified (N = 471 cultures) (*table 2,* Huss and others 1999). Bacteria represented 2.8 percent of the subcultured microorganisms.

We extracted a wide diversity of fungi from the wood samples, including yeast and filamentous forms. Observations of the mode of sexual reproduction or the presence of microscopic structures unique to a phylum (e.g., clamp connections in members of the phylum Basidiomycota) are often necessary to designate the fungal phylum of a culture (e.g., Oomycota, Ascomycota, Basidiomycota), but this was not observed in most of our cultures. Because we could not distinguish phyla, we classified most isolates of filamentous fungi as belonging to the Form-Phylum Deuteromycota (the asexually reproducing or imperfect fungi) or the Phylum

Zygomycota (based on presence of asexual reproductive structures—sporangia) and discuss these separately from the yeasts.

Table 2—*Fungi and other microorganisms recovered from wood samples obtained from woodpecker nest trees in western Washington, 1996-1998.*

Category or species	Number of samples (N = 471)	Percent occurrence
Aspergillus sp.	7	1.49 pct
Bacteria	13	2.76 pct
Basidiomycete #1	9	1.91 pct
Basidiomycete #2	5	1.06 pct
Basidiomycete #3	13	2.76 pct
Basidiomycete #4	1	0.21 pct
Fomitopsis pinicola	21	4.46 pct
Basipetospora sp.	3	0.64 pct
Cladosporium sp.	15	3.18 pct
Fusarium sp.	28	5.94 pct
Gliocladium sp.	6	1.27 pct
Graphium sp.	1	0.21 pct
Mycelia sterilia	11	2.34 pct
Oedocephalum sp.	1	0.21 pct
Oidiodendron sp.	13	2.76 pct
Oomycete (Saprolegniales)	21	4.46 pct
Paeciliomyces sp.	7	1.49 pct
Penicillium sp.	32	6.79 pct
Rhizoctonia sp.	4	0.85 pct
Trichoderma sp. (large-spored)	42	8.92 pct
Trichoderma sp. (small-spored)	27	5.73 pct
Verticillium sp.	2	0.42 pct
Yeast (unknown)	88	18.68 pct
Candida sp.	36	7.64 pct
Cryptococcus sp.	6	1.27 pct
Kloeckera sp.	6	1.27 pct
Rhodotorula sp.	1	0.21 pct
Torulopsis sp.	4	0.85 pct
Unidentified Filamentous Fungus	12	2.55 pct
Zygomycete #1–*Mucor* sp.	20	4.25 pct
Zygomycete #2–*Mucor* sp.	10	2.12 pct
Zygomycete #3	4	0.85 pct
Zygomycete #4–*Absidia* sp.	1	0.21 pct
Zygomycete #5	1	0.21 pct

Yeasts were the most common single type of fungus isolated (29.1 percent, *N* = 211). Based on the API system, a number of these sorted together into subgroups. Most yeasts belonged to the genera *Candida*, *Cryptococcus*, or *Rhodotorula (table 2)* which are among the most common indigenous microorganisms found in soil (Atlas and Bartha 1998). Some species of *Cryptococcus* are associated with the dried fecal material and nesting materials of birds (Rippon 1988). Other genera of yeasts observed included *Torulopsis* and *Kloeckera*.

The remaining fungal isolates (67.3 percent) were filamentous, representing at least 27 distinct fungal types, genera, or species. A large number of the samples represented the group deuteromycetes (Form-Phylum Deuteromycota). Filamentous deuteromycetes isolated and identified included the following genera: *Aspergillus*, *Basipetospora*, *Cladosporium*, *Fusarium*, *Gliocladium*, *Graphium*, *Oedocephalum*, *Oidiodendron* (some cultures may represent the genus *Geotrichum* instead; the culture characteristics of both genera are similar), *Paeciliomyces*, *Penicillium*, *Trichoderma* (two types, differentiated by the production of large and small asexual spores [conidia]), *Verticillium*, and several specimens tentatively assigned to Mycelia Sterilia (i.e., vegetative hyphae with no spores evident) (*table 2*). Some isolates were lacking distinct characteristics and could not be identified to a specific category and thus were listed as unknown. Remaining groups included several species belonging to the Phyla Zygomycota, Oomycota, and Basidiomycota. Each group of zygomycetes and basidiomycetes that were differentiated into subgroups (#1, #2, etc.) were distinctly different from one another, but in most situations, were not identified beyond this level.

Of the basidiomycetes observed during this study, the most commonly encountered was *Fomitopsis pinicola*. We recovered cultures from wood samples and/or observed basidiocarps of *F. pinicola* from 55.1 percent of the nest trees examined (*N* = 78 trees). Basidiocarps of this fungus were found in 47.4 percent, and cultures retrieved from wood samples from 15.4 percent of all trees sampled (*N* = 78). Cultures of this fungus retrieved both from wood samples and basidiocarps were found simultaneously on 7.7 percent of the trees sampled. These data suggest that some nest trees without visible conks are also likely to be harboring colonies of *F. pinicola*. Thus, *F. pinicola* was probably present in woodpecker cavity trees more frequently than we were able to document (55.1 percent) due to sampling error during the retrieval and culture isolation process.

Classification of these fungi into major groups indicates that the predominate fungi found in nest trees or snags are filamentous deuteromycetes and yeasts, but these do not necessarily represent the initial invaders and primary agents of decay in the wood. As an agent of decay, *F. pinicola*, which is a basidiomycete typically causing brown rot, produces digestive enzymes capable of removing cellulose and hemicellulose. The wood shrinks upon drying and cross-checking occurs making the wood brittle (Rayner and Boddy 1988); this probably enables woodpeckers to excavate chunks of material more efficiently compared to wood without decay.

One potential tree pathogen was isolated from one wood sample. At a nest site found outside the primary study sites (not shown in *fig. 1*) we isolated a culture (No. 13-1) which was identified as belonging to the genus *Oedocephalum*. One species in this genus represents the conidial (asexual) state of the basidiomycete *Heterobasidion annosum*, a common cause of butt and root rot in conifers (Agrios 1997, Barnett and Hunter 1998).

We recorded from 1-10 distinct types of fungi with an average of 3.4 fungal types per woodpecker nest tree (*N* = 78). The presence of an ensemble of fungi in decaying wood surrounding a woodpecker nest cavity represents a complex community of organisms with the potential for multiple interactions. Some of these species interactions may be intricately related, such that a succession of fungi move from initial invaders through a series of organisms capable of utilizing various components of wood as these become available over the course of time. Some fungi may enhance the ability of other fungi to grow more effectively through the substratum creating mutualistic associations. Conversely, some fungi may become antagonistic due to the presence of other microorganisms by competing for the same food source. Other organisms may impede the growth of neighboring fungi through the production of waste products or secondary metabolites (e.g., antibiotics, toxins). For example, Atlas and Bartha (1998) and Rayner and Boddy (1988) indicate that species of the soft-rot fungus *Trichoderma* are antagonistic to the growth of other fungi. Additionally, some fungi may exist as parasites or predators on other organisms present in the wood (e.g., nematodes, other fungal species). For example, cultures No. H97-14-1A and H97-14-2A (two unidentified fungi) were observed to be parasitizing either another fungal colony, a co-inhabitant in a mixed culture, or themselves (self-parasitism). Self-parasitism has been documented in other wood-decaying fungi (e.g., *Stereum hirustutm*), but the biological significance of this phenomenon is unknown (Rayner and Boddy 1988).

Many of the fungi identified represent soft-rot fungi (Rayner and Boddy 1988) that primarily live off carbohydrates (e.g., hemicellulose, cellulose) found in moist wood or by-products of decay that leach into the wood through the activities of other microorganisms. These fungi may represent a succession of fungi that grow into the wood after gaining entrance in the heartwood and sapwood through the activities of primary wood-decay fungi (e.g., white rot and brown rot fungi), fungal pathogens, animal vectors (e.g., foraging woodpeckers), and/or wood-inhabiting and wood-boring insects in injured living or dead trees. The relative abundance of secondary invaders into the wood and the establishment of a decay community in our samples suggests that the presence of this community also softens wood and facilitates the establishment of nest cavities by woodpeckers. We suggest that initial decay of trees is caused by a basidiomycete, such as *Fomitopsis pinicola*, which sets the stage for secondary invasion by a variety of soft-rot fungi and yeast species. The collective decay caused by this suite of organisms may then facilitate excavation of cavities by woodpeckers. It is possible that the introduction of a variety of fungal organisms, and not just one species, could expedite the use of trees by woodpeckers.

Experimental Tree Inoculations

In 1997 and 1998, we completed inoculation of 650 trees, fulfilling the original experimental design *(table 1)*. Fifteen of the inoculated stands were on Rayonier lands, nine on lands managed by the Department of Natural Resources, four on I. P. Pacific Timberlands Inc. lands, four on Weyerhauser lands, and two on John Hancock Timber Resource Group lands *(fig. 2)*. During the summers of 1997 and 1998, we inoculated 65 clusters of 10 trees each within 34 separate managed forest stands *(table 3)*. A total of 650 trees were inoculated, 330 with viable fungus and 320 trees served as controls and were inoculated with blank dowels. At one stand, we determined that the treatment cluster (T97-04; see Huss and others 1999) was most appropriately classified as a small-diameter tree stand with snags, but that the nearby control cluster (C97-04) contained too few snags. Therefore, two additional small-diameter stands were located at another site with compatible characteristics to complete the pairing for those two mismatched clusters.

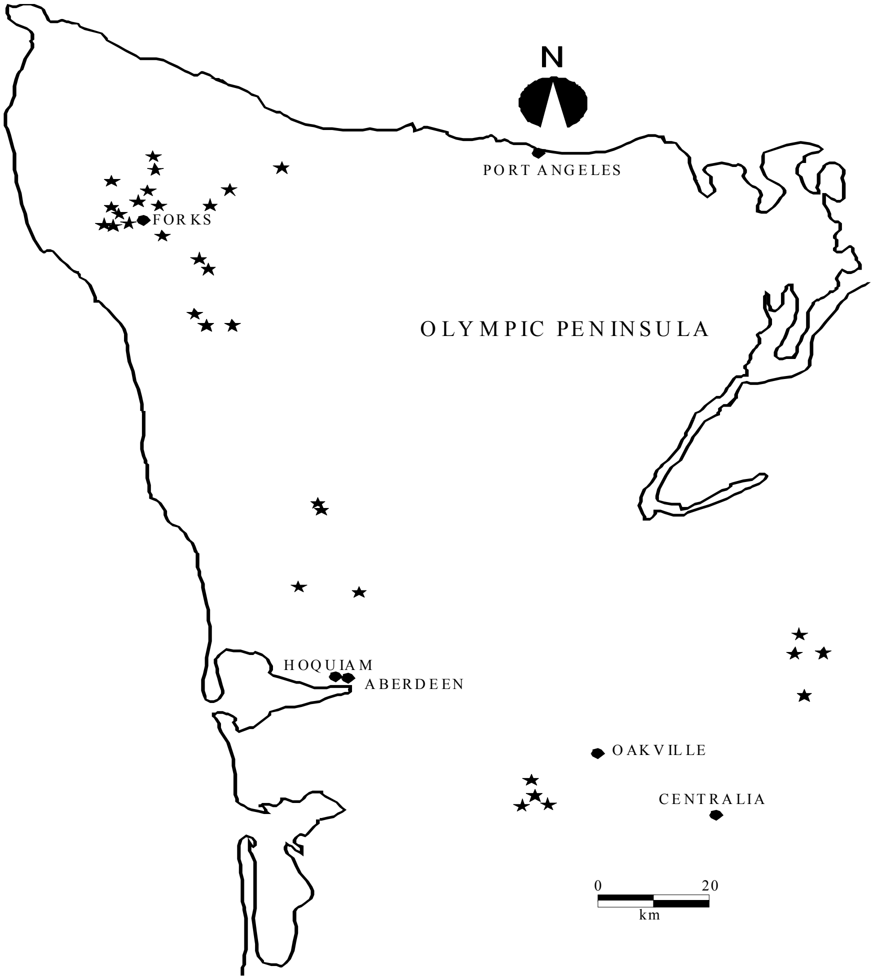

Figure 2—Location of fungal inoculation sites (identified by stars) in western Washington. Sites are on land owned by Rayonier (*N*=15), the State of Washington (managed by the Department of Natural Resources; *N*=9), I. P. Pacific Timberlands Inc. (*N*=4), Weyerhaeuser (*N*=4), and John Hancock Timber Resources Group (*N*=2).

Table 3—*Summary of experimental inoculation treatments and controls completed during 1997 and 1998 in western Washington. Each cluster involves the inoculation of 10 trees.*

Stand classification for experiment	Treatment cluster	Control cluster
Western Hemlock		
Large-diameter trees with snags	4	4
Large-diameter trees with few snags	4	4
Small-diameter trees with snags	4	4
Small-diameter trees without snags	5	4
Douglas-fir		
Large-diameter trees with snags	4	4
Large-diameter trees with few snags	4	4
Small-diameter trees with snags	4	4
Small-diameter trees without snags	4	4

In the process of searching for stands with suitable characteristics, we discovered that the age of a stand is not always directly correlated with mean tree diameter. For example, one stand (T97-05 and C97-05) had relatively small diameter trees, but was 147 yr old. We have classified that stand as a small-diameter tree stand with snags. Despite these exceptions, large diameter/older stands were on average 71 yr old, whereas small diameter/younger stands typically averaged less than 51 yr in age *(table 4).* To facilitate efficient climbing, workers generally inoculated trees with the largest diameter (usually > 35 cm dbh) in small-diameter classified stands and the relatively small-diameter trees (< 50 cm) in large-diameter classified stands. Despite these opposing biases, inoculated trees in small diameter stands (0 dbh = 39 cm) were clearly smaller than the trees inoculated in large-diameter stands (0 dbh = 45 cm; *table 4).* These differences in tree diameters between older stands and younger inoculated stands were statistically significant ($P < 0.001$, $t = 4.8$ for comparison of treated plots, $N = 33$; $P < 0.01$, $t = 3.1$ for comparison of control plots, $N = 32$).

Table 4—*Mean characteristics of forest stands inoculated with* Fomitopsis pinicola *in western Washington, 1997 and 1998.*

	Treatment stands			**Control stands**		
	Mean[1]	**(N)**	**Range**	**Mean[1]**	**(N)**	**Range**
Large diameter/older stands						
DBH (cm)	46.9	(16)	37.7-60.2	44.8	(16)	38.3-61.0
Age (years)	71.4	(16)	49-197	71.4	(16)	49-197
Small diameter/younger stands						
DBH (cm)	38.9	(16)	31.1-49.9	38.9	(16)	30.6-44.8
Age (years)	50.8	(16)	30.0-147.0	51.8	(15)	30.0-147.0

[1] Values were derived from trees treated and may not be representative of average tree characteristics in stand.

Two classes of stands were particularly difficult to locate: larger tree diameter stands without snags and smaller tree-diameter stands with snags. These stand criteria are somewhat contrary to natural succession patterns. Later successional-stage forests generally exhibit some mortality and thus are very likely to contain a conspicuous number of snags. Conversely, early successional-stage forests normally have relatively little tree mortality coupled with the fact that small-diameter snags are often not persistent and fall over after a few years. For this reason, we accepted some stands in these two categories that only marginally fit our original study plan. The most difficult stand criteria to meet were older/large diameter tree stands with no snags. We will examine samples of inoculated trees at 3-yr intervals and determine if cavity-nesting species have colonized these sites.

Establishment of Fomitopsis pinicola *in Inoculated Trees*

One to three years after inoculation of trees with *F. pinicola*, fungal mycelia have been observed in some trees around the entrance of the original inoculation hole created when we introduced the fungus into the wood. The formation of basidiocarps or conks consistent with the morphology of this species was also observed in 2000 *(fig. 3),* emerging from the bark just below the point of initial inoculation. Of 20 randomly selected trees inoculated in 1997 and sampled in 1998, *F. pinicola* (red-belted conk), was retrieved from 14 (70 percent). Of the trees sampled in 1999, 20 inoculated in 1997, and 18 inoculated in 1998, the success rate of retrieving the introduced fungus was 50 percent in both cases. We only took one wood sample from each tree; consequently, even trees from which *F. pinicola* was not recovered, it is likely that this fungus was successfully introduced into at least a few of these and missed by us during the retrieval and culture isolation process. Once it was determined that a tree possessed *F. pinicola*, we tested whether or not the strain recovered matched the strain introduced (i.e., 64A or 36A). Based on vegetative compatibility analysis, 100 percent (N = 33) of the samples collected matched the fungal isolate introduced previously into that tree *(fig. 4).* These results demonstrate that the fungal inoculations are largely successful (greater than or equal to 50 percent to 70 percent success) in introducing the desired fungus into both western hemlock and Douglas-fir.

Figure 3—Basidiocarp of the red belted conk *(Fomitopsis pinicola)* seen emerging from surface of a living western hemlock tree (T97-01-02) inoculated in 1997 (3-years post treatment).

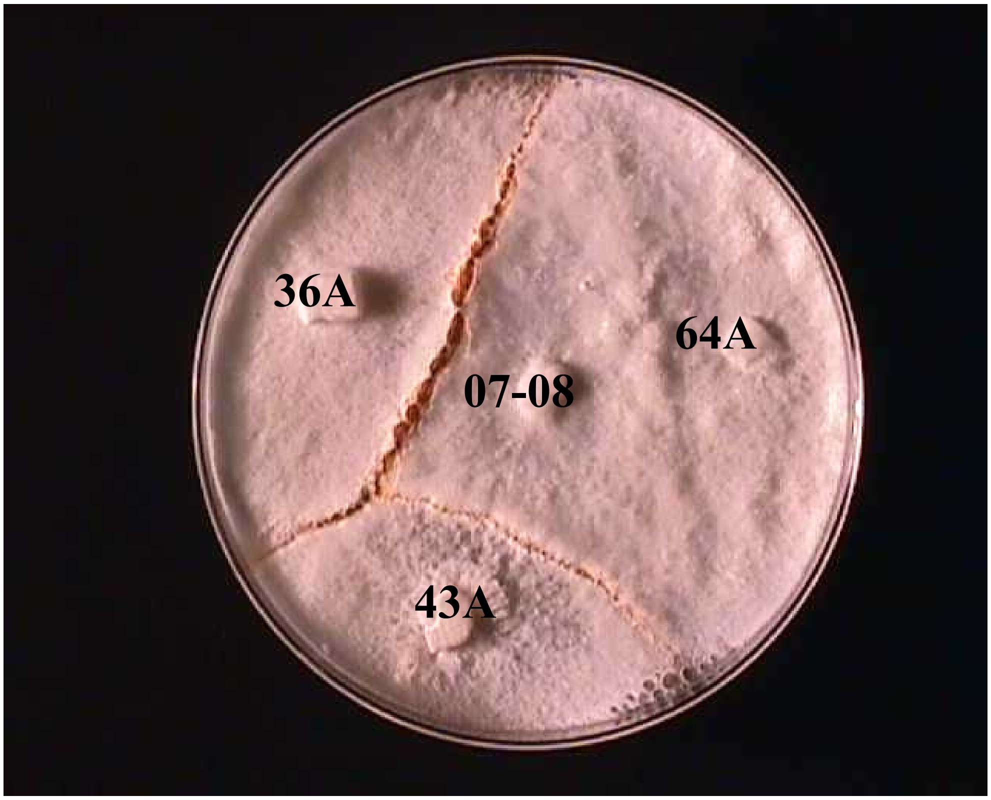

Figure 4—Pairing between isolates recovered from wood in 1998 (central colony) with trees inoculated with *Fomitopsis pincola* (64A) in 1997 with three test strains (peripheral colonies—36A, 43A, and 64A). Isolate 07-08 retrieved from wood is compatible with culture 64A but not with the other two peripheral cultures.

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Characteristics of Log Resources in Northeastern Oregon: Case Studies of Four Management Treatments[1]

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Abstract

Logs have complex physical, biological, and functional attributes. The body of literature with detailed empirical data on log resources in diverse habitats in the Interior Columbia River Basin is sparse. Sampling schemes developed by the USDA Forest Service for assessing logs as woody fuel usually have translated amounts of logs into weight or volume per unit area (tons or ft^3 per acre). To depict amounts of logs in a more descriptive way—to assess wildlife habitat, for example—log resources may be more adequately described in terms of density, percentage cover, mean length, and combined length of logs per unit area, in addition to weight and volume. Sampling data are presented on log resources in the Blue Mountains of northeastern Oregon, which are compared to the standards set forth in the Pacific Northwest Regional Forester's Eastside Forest Plan Amendment No. 2, Alternative 2, for establishing riparian, ecosystem, and wildlife standards for timber sales. Data from four case studies are presented that characterize log resources in harvested and unharvested mid- and late-structure mixed conifer and ponderosa pine stands. Two case studies describe log resources in three stands before and after salvage harvest to reduce fuels, but maintain large-diameter logs. Post-salvage numbers of logs ($\geq$ 15 cm large-end diameter) per ha were 58 to 80 percent higher than pre-salvage densities. The proportion of large logs ($\geq$ 30 cm large-end diameter) among all logs remaining after salvage declined by 3 and 10 percent in two stands and increased 6 percent in one stand. Tonnage of logs increased by 4, 7, and 54 percent in the salvaged stands. Breakage of logs from felling and heavy equipment resulted in reductions in log lengths from about 8 m pre-salvage to 5 m post-salvage. Post-salvage amounts of log resources observed in all the harvested stands were generally higher than prescribed by the Eastside Forest Plan Amendment No. 2.

Introduction

Coarse woody debris (CWD) in all its forms has important physical, chemical, and ecological values in healthy forests. These values are well documented elsewhere in these proceedings (Laudenslayer and others 2002). However, what is largely unknown about CWD in general, or logs in particular, is how much is needed to support the complex of ecological functions dependent upon this stratum. A fundamental aspect of understanding ecological functions in a particular stratum such as logs is having the tools to quantify or otherwise describe that resource.

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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Appropriate log sampling techniques must be able to cope with an array of variables over a wide range of densities and distributions, and that will describe the log resource in ways that have relevance to managers with a broad spectrum of biophysical and socio-economic views of what a forest ecosystem should be or do. Because fire behavior and management are affected significantly by the abundance, distribution, and size characteristics of CWD, considerable energy has been devoted to portraying amounts of CWD as fire fuels (Brown 1974; Fischer 1981a, b; Koski and Fischer 1979; Maxwell and Ward 1976, 1980; Walstad and others 1990). Fuels specialists in the USDA Forest Service have typically described CWD in terms of tonnage (short tons) or volume (ft^3) per acre. But for the wildlife biologist who wants to assess log resources in ways that are relevant to wildlife, these two parameters are not very descriptive or useful. For example, tonnage is not a particularly relevant parameter for defining requirements for rodents whose numbers are related to percentage of the forest floor covered by CWD (Carey 2000, Carey and Johnson 1995, Wilson and Carey 2000). Similarly, quality of foraging habitat for pileated woodpeckers has been found to be related to density and size-class distribution, not tonnage, of logs in home ranges (Bull and others 1997, Torgersen and Bull 1995). Other forest professionals—mycologists, silviculturists, soil scientists, fire ecologists, economists, or logging engineers—will have their own views of useful descriptive parameters, and ways of looking at CWD as resource or risk.

With the broadening appreciation for the values of CWD, management is being called on to both quantify these resources, and to provide guidelines for its management in planning documents. In the Forest Service's Pacific Northwest Region, one such planning document is the Regional Forester's Eastside Forest Plan Amendment Number 2, Alternative 2. This directive was issued as a "Decision Notice for the Revised Continuation of Interim Management Direction Establishing Riparian, Ecosystem, and Wildlife Standards for Timber Sales" (Lowe 1995). The Decision Notice identified interim vegetative structural stages for ecosystem standards, and clarified wildlife standards (hereafter referred to as the "Standards") for nine National Forests on the east side of the Cascade Mountains in the Pacific Northwest. These Standards are being applied pending completion of an Eastside Ecosystem Management Strategy for the Pacific Northwest Region. A portion of the Decision Notice identifies the need for snags and down logs for wildlife nesting, roosting, and feeding. The Standards stipulate appropriate amounts and sizes of logs in specific stand types. *Table 1* shows the prescribed Decision Notice Standards, and their approximate metric equivalents, for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), mixed conifers, and lodgepole pine (*P. contorta* Dougl. ex Loud.) stand types.

Embedded in these Standards are four terms for expressing amounts of log resources; three of which bear explanation. One of the implicit terms might be called "minimum log size." The Standards stipulate that logs under consideration in mixed-conifer and ponderosa pine stands shall be >6 feet long (1.8 m) and ≥12 inches (30.5 cm) in diameter at the small end. For convenience, such logs will be referred to here as "qualifying logs." The three explicit terms used to describe qualifying logs in the Standards are "diameter at small end," "total lineal length," and "pieces per acre."

Table 1—*Log standards as presented in the Regional Forester's Eastside Forest Plan, (Lowe 1995).*

Stand type	Pieces per acre	Diameter at small end	Piece length	Total lineal length
Ponderosa pine	3-6 (7-15 per ha)	12 in. (30 cm)	>6 ft. (2 m)	20-40 ft. (6-12 m)
Mixed conifer	15-20 (37-49 per ha)	12 in. (30 cm)	>6 ft. (2 m)	100-140 ft. (30-43 m)
Lodgepole pine	15-20 (37-49 per ha)	8 in. (20 cm)	>8 ft. (2.5 m)	120-160 ft. (37-49 m)

"Diameter at small end" may be misleading because it does not refer to the actual small end of the log. For example, given a ponderosa pine log that is 11 m long, 50 cm in diameter at its larger end, and 20 cm at its smaller end, the stipulated 30.5 cm (12 inches) "small end diameter" is not an "end" at all, but the place along the log's length at which the log is 30.5 cm. This is a relevant point in explaining the term—"total lineal length." First, only qualifying logs in terms of minimum piece-length and diameter can contribute to total lineal length. In the above example of the 11-m-long ponderosa pine log, only about 7.15 m would count toward its qualifying "lineal length" because only that much of the log is equal to or greater than the stipulated 30.5 cm "small end diameter." The sum of the qualifying lineal lengths[3] of individual logs in a stand or sampling unit contributes to "total lineal length" per acre. "Pieces per acre" is simply an expression of the number per acre of log pieces of the stipulated qualifying size.

Empirical data that present log resources in terms of the explicit log descriptors used in the above Standards are scarce. In fact, there are also no well-established sampling protocols for estimating either number of logs or their total lineal length per unit area. Computer outputs for Forest Service fuels inventories that are conducted with the line-intersect sampling protocols of Brown (1974) routinely express log resources as tonnage and weight, not in terms of density or total lineal length. To determine the parameters stipulated in the Standards, the line intersect sampling protocols would have to be expanded to include at least log lengths and large-end diameter (LED) of intersected logs. Log-taper factors for particular species of logs could then be used to calculate total qualifying lineal length of logs. If samplers added small-end diameter (SED) to the measurements collected during line-intercept sampling, then total lineal length could be calculated using one or more appropriate formulae.[3] But the point is that these additional measurements are not now routinely being collected.

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[3] The amount of qualifying length (m) in a log may be calculated by using the following equation: QL = TL (BPD – LED / SED – LED); where QL is qualifying length of a log; TL is total log length; BPD is the qualifying break- point-diameter, e.g. 0.305 m (12 inches); LED is large end diameter; and SED is small end diameter of the log. All dimensions in meters. Example: If TL = 11m; BPN = 0.305m; LED = 0.50m; and SED = 0.20m; then QL = 7.15m.

The objectives of this paper are to describe log resources in selected mixed conifer and ponderosa pine stands, before and after treatment, under four management scenarios, and to compare this new information with the Standards for log retention as set forth in the Region 6 Decision Notice. For these comparisons I will use log resource descriptors from four case studies of selected stand types and treatments in northeastern Oregon: 1) in late-structure stands 40 years after selective harvest; 2) before and after salvage/fuel-reduction harvest; 3) before and after a fuel-reduction harvest to conserve late-structure large trees; and 4) after selection harvest and prescribed underburn.

Study Areas and Methods

The forest stands we examined are all in the Blue Mountain Province in northeastern Oregon. For the log inventories reported here, logs had to be $\geq$ 15 cm (6 inches) at their large end and $\geq$ 2 m (6.6 feet) long. For each log, whether in fixed-area plots or on transects, we recorded large-end diameter (LED) and small-end diameter (SED) to the nearest cm, and length to the nearest m. Decay class was tallied to determine weight of logs (Brown and See 1981). Smalian's formula (Wenger 1984) was used to compute volume. When line-intercept sampling was used (as in case study 4), the equations of DeVries (1973) were used to calculate log variables on a per ha basis.

Log resources are presented in terms of the traditional variables of volume and tonnage per unit area as used in fire fuels inventories. Density, mean length of logs, and total lineal length of logs per ha are presented because these are the variables stipulated in the Standards. Total lineal length of logs was obtained by first calculating the amount of qualifying length in each log,[3] and adding the qualifying lengths to obtain total lineal length per unit area. Although inventories of log resources do not routinely use density as an expression of measurement, this variable is used in the Standards and in some studies of wildlife use of logs (Bull and others 1995, 1997; Torgersen and Bull 1995). Percent cover of logs was added as a variable to describe log resources because of the wide use of this variable to describe habitat for small mammals (Buchanan and others 1999, Carey and Johnson 1995, Carey and others 1999, Wilson and Carey 2000). This variable is also referred to as projected area or projected cover (Caza 1993, Harmon and Cromak 1987, Marshall and others 2000).

Differences between log resources before and after salvage harvesting were tested using the t-test (SPSS software).[4]

Case 1—Late-structure Stands

Study stands were selected in the Five-Lock Forest Demonstration Area on the Umatilla National Forest about 20 km west of Ukiah, Oregon. Twelve stands were chosen to represent three stand types: 1) designated old-growth mixed conifers; 2) mid- to late-structure mixed-conifers; and 3) late-structure ponderosa pine. These stands were relatively natural, i.e., without recent harvest entries. The term "natural" for characterizing these stands is used advisedly because virtually all of the stands

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[4] Mention of trade names or products is for information only and does not imply endorsement by the U.S. Department of Agriculture.

had some selective harvesting for the largest ponderosa pine and Douglas-fir about 40 years ago. Also, fire control would certainly have altered fire-return intervals compared with patterns existing prior to the time of European settlement in the 19th century. Each of the three stand types was represented by four study stands 5-12 km apart. Within each of the four 10-15 ha stands there were ten randomly located 20 x 20-m plots on which log inventories were conducted.

Case 2—Salvage/Fuel-reduction Harvests

One mixed-conifer stand each was located in the MacKay and Lane Creek drainages of the Wallowa-Whitman and Umatilla National Forests 30 and 50 km west of La Grande, Oregon. These 12 and 15 ha stands had mid- to late-structure Douglas-fir (*Pseudotsuga menziesii* [Mirib.] Franco) and grand fir (*Abies grandis* [Dougl. ex D.Don] Lindl.), with minor amounts of ponderosa pine and western larch (*Larix occidentalis* Nutt.). Both stands had suffered heavy defoliation in the course of a western spruce budworm (*Choristoneura occidentalis* Free.) outbreak from 1980-1992 (Scott and Schmitt 1996). The heavy mortality sustained in these two areas prompted District managers to prescribe salvage sales in 1996 to both reduce fuels and to maintain late and old structural components of large-diameter live and dead trees and logs. The prescription stipulated that only dead or dying trees with less than 50 percent live crown and < 38 cm (15 in.) dbh could be harvested. Large logs with the same minimum large end diameter were also to be left. In 1994, we did a comprehensive pre-salvage log inventory in each of the stands. We sampled 20 and 30 randomly distributed 10 x 10-m plots at the Lane and MacKay stands, respectively. In 1996, we conducted a post-salvage inventory on the same plots to characterize changes in log resources. In each plot, we measured all logs with a large-end diameter (LED) $\geq$15 cm, a minimum length of 2 m, and whose mid-length-point lay within the plot boundaries.

Case 3—Fuel-reduction Harvest to Retain Old-growth Characteristics

This site was at Frog Heaven on the Umatilla National Forest about 42 km southwest of La Grande. This stand was the subject of a study reported by Bull and others (1995), in which the management objective was to protect old, large-diameter living and dead stems by lowering fire risk, and to encourage regeneration. The study was laid out within harvest units designed to examine the effects of a fuel-reduction treatment to protect late-structure stands that had a heavy component of large trees. There were several large trees in these stands that were nesting or roosting trees for pileated woodpeckers *(Dryocopus pileatus)* and had been used for several years by nesting Vaux's swifts *(Chaetura vauxi).* The stand had sustained repeated heavy defoliation by the western spruce budworm during a local outbreak from 1980-1992 (Scott 2000). Mortality of many trees of all ages in the site had created a high risk that any fire would completely destroy the old-growth character of the site in an area that had few stands with large-trees and/or large-log structural components. This study site was represented by three stands: two contiguous stands of about 8 ha each that would be harvested in 1994 to reduce fuel-loading, and one untreated control stand of 22 ha. Sampling was done within 10-m-wide belt transects that were divided into contiguous 10-m-long plots. The belt transects were laid out along random azimuths such that they were completely within the study stands. There were 750 m

(75 plots) of belt transect in the treated stands and 400 m (40 plots) of belt transect in the control stand. The same log parameters as for the other studies were collected and summarized on the basis of treatment. Pre-treatment sampling was done in the fall of 1993; salvage logging was done during the ensuing winter of 1993-94 when the forest floor was snow-covered; and post-treatment sampling was done in the summer of 1994. We prescribed harvest activities be conducted only when the ground and logs were snow-covered to minimize log breakage. Previous experience had shown us that the activity of harvesting equipment on bare logs resulted in undue breakage. For this paper, summaries of log resources were combined for the two treated stands, and the control stand was summarized alone. Because this study was completed and published before the Standards were established in 1995, the original data were reanalyzed to produce specific information that would permit meaningful comparisons with the Standards.

Case 4—Selection Harvest/Underburn in Ponderosa Pine

Twelve study stands, approximately 15-75 ha each, were within the La Grande Ranger District, Wallowa-Whitman National Forest, in northeastern Oregon. The stands were equally divided between two areas in the drainages of the upper Grande Ronde River and Spring Creek. Stands were 25-30 km east and south of La Grande. These drainages are dominated by extensive stands of ponderosa pine and mixed conifers. All of the stands had been underburned between 1993 and 1996, and were classified by District silviculturists as being in the understory reinitiation structural stage of Oliver and Larson (1990). The underburn treatment was designed to favor ponderosa pine and western larch by reducing encroachment of Douglas-fir and true firs in the understory. Log sampling was done in 1998. Twenty sampling points spaced at 30-m intervals along randomized transect lines were used to characterize log resources in each of the 12 stands. Each sampling point became the center for three 20-m-long radiating transects along which logs were tallied. Each of the radiating transects was begun 2 m from the plot center. This arrangement yielded 60 m of log-sampling-transect per plot; 1200 m per stand. We tallied each log that was intercepted by a transect.

Results and Discussion

Case 1—Late-structure Stands

Log inventories in the Five-Lock late- and old-structure mixed-conifer and ponderosa pine stands *(table 2)* showed high densities of both large ($\geq$ 30 cm LED) and small ($\geq$15 cm LED) logs, and moderately high densities of large logs as compared with the other cases reported here (cf. *tables 3-5*). These Five-Lock stands have remained largely undisturbed by harvesting for about 40 years. However, in the old-growth sites and the mid- to late-successional mixed conifer sites, quantities of Douglas-fir and grand fir logs were presumably generated as a result of the budworm outbreak of 1980-92. The densities of 59-79 large logs per ha we recorded there are substantially higher than the 37-49 per ha post-harvest densities prescribed in the Standards for mixed conifer stands *(table 1).* This suggests that well-timed salvage or fuel-reduction harvests might have been prescribed on the grounds of reducing amounts of CWD, and thereby diminish fire risk and hazard. Research by Bull and Holthausen (1993) determined that there were about 240 logs per ha in the pileated woodpecker home ranges that included the very same stands that we inventoried for this case. Using an approximate value of 35 percent large logs (Torgersen and Bull 1995) would yield about 84 large logs per ha within those home ranges. This is close to the range we determined for these stands. The relationship of the densities of 59 and 79 large logs per ha to the 84 logs per ha observed by Torgersen and Bull (1995) is unclear. They may be either functionally lower or may be approaching an acceptable number for use by pileated woodpecker.

Table 2—*Log resources on the Five-Lock Demonstration Area, North Fork John Day Ranger District, Umatilla National Forest, Forest Service, U.S. Department of Agriculture, 1993.*

	Logs ≥ 15 cm in large-end diameter						**Logs ≥ 30 cm LED[1]**	**Logs ≥30 cm SED[2]**
Stand Type	**Logs per ha**	**Percentage cover**	**m^3 per ha**	**Metric tons per ha**	**Total lineal length (m) per ha**	**Mean log length (m)**	**Logs per ha**	**Total lineal length (m) per ha**
Old-growth	[3]220 (28.2)	6.2	149	48	2,223	10.1	59	206
Mixed conifers	225 (37.1)	5.4	124	40	1,886	8.4	79	183
Ponderosa pine	115 (10.8)	1.5	38	12	658	5.7	25	47

[1] large-end diameter

[2] small-end diameter

[3] standard error in parentheses

With mean log lengths of 8.4-10.1 m, our sites had about 183-206 m of total lineal length of qualifying logs. Home ranges of pileated woodpeckers studied by Torgersen and Bull (1995) and Bull and others (1997) had total lineal lengths of qualifying logs between 294-362 m per ha. These amounts contrast with the 30-43 m of total lineal length prescribed in the Standards. However, it should be mentioned that the Standards were not designed to specifically provide amounts of CWD that would support pileated woodpeckers. Given the contrasts between the Standards and use of the Five-Lock stands by pileated woodpeckers, as well as those reported in the literature for foraging habitat by pileated woodpeckers, managers need to be informed about the presence and needs of certain wildlife species in stands for which harvest prescriptions are planned. Unfortunately, quantitative information about the log-resource requirements for most species of wildlife is not available.

In the Five-Lock ponderosa pine stands, the density of 25 qualifying large logs per ha was much higher than the 7-15 logs per ha prescribed in the Standards. There had been no major insect or fire disturbances in the ponderosa pine stands that corresponded to the budworm outbreak in mixed conifers that would have accounted for these amounts of CWD. Thus, despite harvesting operations with emphasis on removing large pines 40 years ago, there were, nonetheless, relatively large amounts of qualifying CWD as a consequence of normal recruitment from standing trees and snags. Control of fire undoubtedly played a role in maintaining larger amounts of CWD that might otherwise have burned under pre-settlement fire-return intervals.

Case 2—Salvage/Fuel-reduction Harvests

In the aftermath of the western spruce budworm outbreaks and the subsequent activity of the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) and fir engraver beetle (*Scolytus ventralis* LeConte) in northeastern Oregon from 1980-1992 (Scott and Schmitt 1996), there were vast acreages of standing dead trees that are continually falling and adding to fuel-loading and risk of fire. Because of an active market for chips, many harvest sales were designed to salvage the standing dead volume to diminish the potential for adding further to fuel-loading, especially in mixed conifer stands. This case study followed two such stands in which Forest Service District managers chose the management option of salvaging standing dead trees and removing smaller down logs that were contributing to fuel loading. Prescriptions for these harvests were written with the intent of maximizing the retention of large snags and large logs for their wildlife values, but to remove smaller snags and logs that represented a present or future risk as fuel for wildfire. *Table 3* and *Figure 1* show how amounts of CWD changed between pre-harvest and post-harvest in the Lane and MacKay harvest units. Post-harvest measures of CWD changed in relevant ways. The numbers of all logs remaining post-harvest was significantly higher in Lane ($n = 20$, $t = -3.22$, $p = 0.004$) and MacKay ($n = 20$, $t = -2.65$, $p = 0.016$). The number of large logs increased, but not significantly so. Conversely, the proportional representation of large logs among those remaining on the ground declined slightly. Percentage cover, volume, and tonnage increased only modestly; varying from 1-14 percent (*table 3, fig. 1*).

Table 3—*Log resources before and after a salvage harvest to reduce fuel-loading in two stands with heavy tree mortality resulting from a 12-year outbreak of western spruce budworm (*Choristonerua occidentalis *Free.), in northeastern Oregon, Wallowa-Whitman and Umatilla National Forests, Forest Service, U.S. Department of Agriculture, 1994, 1996.*

	Logs ≥ 15 cm in large-end diameter						Logs ≥ 30 cm LED[1]	Logs ≥30 cm SED[2]
Stand (year)	**Logs per ha**	**Percentage cover**	**m^3 per ha**	**Metric tons per ha**	**Total lineal length (m) per ha**	**Mean log length (m)**	**Logs per ha**	**Total lineal length (m) per ha**
Lane Creek (1994)	[3]205 (82.3)	2.9	73	23	1,385	6.8	59	132
Lane Creek (1996)	350 (140.5)	3.3	75	24	1,451	4.1	67	140
MacKay Creek (1994)	385 (156.4)	5.6	95	30	3,565	9.2	37	132
MacKay Creek (1996)	610 (246.3)	6.0	101	32	3,355	5.4	42	197

[1] large-end diameter

[2] small-end diameter

[3] standard error in parentheses

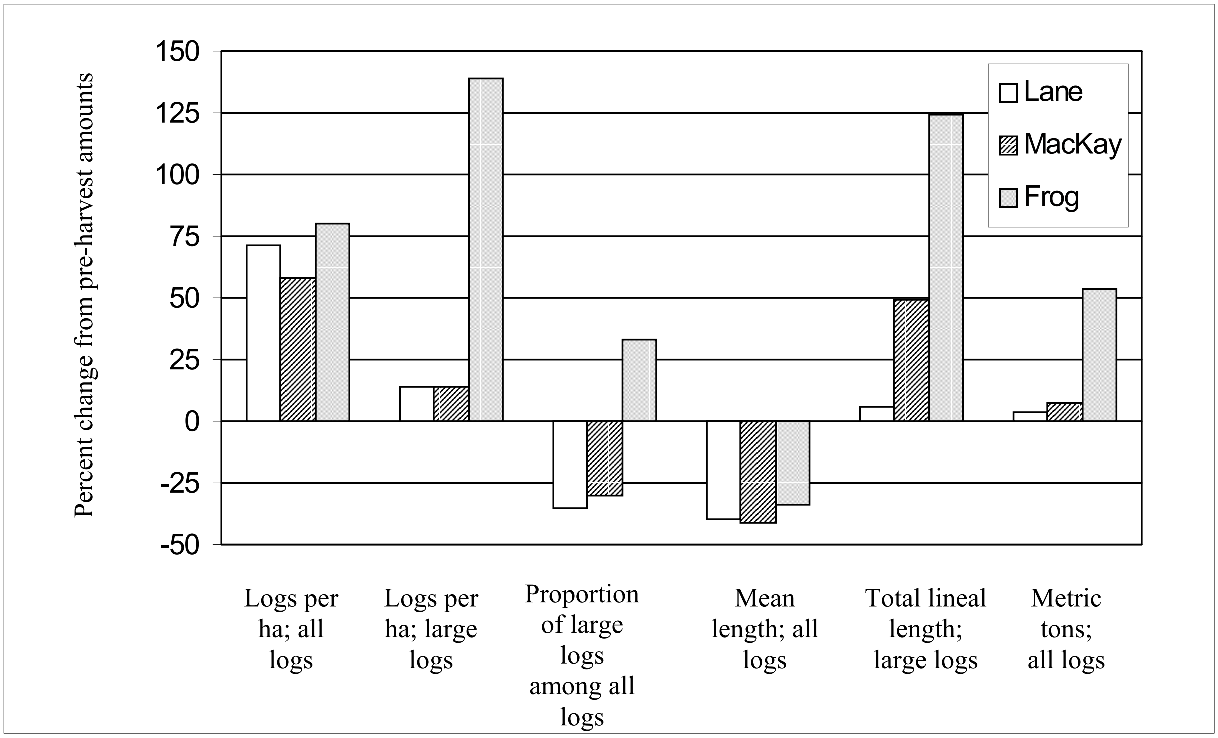

Figure 1—Percentage change between pre- and post-harvest descriptors of log abundance in selected stands treated with fuel-reduction harvests, Umatilla and Wallowa-Whitman National Forests, 1993-1994. "All logs" refers to logs $\geq$ 15 cm in large-end diameter; "large logs" are those $\geq$ 30 cm in large-end diameter.

For these two stands, log density alone would have been a poor descriptor of harvest effects on CWD because harvest activity created more but shorter pieces of wood than were present pre-harvest. In the MacKay units, post-harvest log lengths were significantly (n = 20, t = 3.83, p = 0.001) only about half as long as those at pre-harvest (5.4 vs. 9.2 m). In the Lane Creek unit, post-harvest log lengths were about two-thirds as long as pre-harvest log lengths (4.1 vs. 6.8 m), which was only a marginally significant difference (n = 20, t = 2.21, p = 0.041). Taken together, post-harvest log lengths in these units were about 40 percent as long as pre-harvest lengths *(fig. 1)*.

The measures of success of these harvests in terms of their having retained the prescribed desired large log component are mixed. Specifically, the absolute numbers of large logs ($\geq$ 30 cm in LED) per unit area were increased by 14 percent post-harvest, but not statistically significantly so. The percentage composition of large logs among the residual logs was about a third less than at pre-harvest. Percentage composition of large logs among all residual logs fell from 10 percent to 7 percent at MacKay, and from 29 percent to 19 percent at Lane. In something of the same manner as for density of logs, the absolute number of linear meters of these large logs increased by 6 and 49 percent at Lane and MacKay. The proportions of total lineal meters of large logs among all logs remained about constant, at about 5 and 10 percent for MacKay and Lane, for pre- and post-harvest samples, but the changes were not significant in either case. Tonnage of logs was only marginally and nonsignificantly higher post-harvest but was represented mostly in the smaller diameter classes as opposed to the desired larger classes of logs ≥30 cm *(table 3, fig. 1)*. In the overall sense of what sizes and amounts of logs were left at post-harvest, the intent of these salvage harvests did not meet expected goals. However, given that most of the small-diameter standing dead material was salvaged and that the large standing dead trees were retained, then it could be argued that recruitment will come from this desired large-diameter standing dead component.

Case 3—Fuel-reduction Harvest to Retain Old-growth Characteristics

The Frog Heaven site was a designed experiment used to study the potential to reduce fuels in a late-structure stand with many large legacy trees while still maintaining old growth structural components. The unharvested control site showed a large increase in log resources, from 215 to 335 logs per ha, over the course of one season: 1993-1994. This was due to some high wind events that brought down many of the dead trees in the stand. Percent cover in the control sites increased by only 1 percent, but volume and tonnage increased dramatically. Windthrow and breakage were not confined to smaller trees; density of large logs increased twofold, and total lineal length of large logs increased about 40 percent, from 237 to 332 m per ha *(table 4)*.

Table 4—*Log resources after harvest of dead components to reduce fuel-loading and accelerate regeneration in old-growth stands occupied by nesting pileated woodpeckers and Vaux's swifts in northeastern Oregon. Frog Heaven site, La Grande Ranger District, Wallowa-Whitman National Forest, U.S. Department of Agriculture, 1993, 1994.*

	Logs ≥ 15 cm in large-end diameter						Logs ≥ 30 cm LED[1]	Logs ≥30 cm SED[2]
Treatment (year)	**Logs per ha**	**Percentage cover**	**m^3 per ha**	**Metric tons per ha**	**Total lineal length (m) per ha**	**Mean log length (m)**	**Logs per ha**	**Total lineal length (m) per ha**
Pre-salvage (1993)	314	5.6	109	35	3,080	9.5	57	220
Post-salvage (1994)	566	7.4	168	54	3,754	6.3	136	493
Control (1993)	215	4.3	101	32	1,830	8.5	57	237
Control (1994)	335	5.3	165	52	2,160	6.4	106	332

[1] large-end diameter
[2] small-end diameter

In the salvaged stand, the increase in overall log density from 314 to 566 logs between pre- and post-salvage was statistically significant ($n = 75$, $t = -7.33$, $p = <0.001$) and is no doubt attributable, in part, to the same wind events of the intervening winter of 1993-94. Percent cover, volume, and tonnage all increased in much the same way as the control stand. Despite the effort to minimize log-breakage by confining harvesting activity to the period when there was snow cover, mean log length was nonetheless reduced significantly (n = 75, t = 4.36, p = <0.001) in the harvested stands, and as compared with the control stand (33 vs. 25 percent shorter logs), presumably because of the activity of harvesting equipment. The density of large logs in the harvested stands increased statistically, from 57 to 136 logs per ha (n = 75, t = -2.95, p = 0.004), compared to large-log density in the control stand where it increased from 57 to 106 logs per ha *(table 4, fig. 1).* Some of this increase in the harvested stand might be attributed to the wind events of the winter, and not solely to the logging activity. We observed that many of the larger trees, which were intended to be left standing, were brought down in the process of felling the smaller trees as prescribed. It is interesting how closely the densities of large logs in the late- and old-structure mixed conifer stands of Case 1 *(table 2)* approximate those in the pre-treatment year (1993) at the old-growth stands of Case 3 *(table 4).*

Because this management case at Frog Heaven was carried out in a research context, there was greater oversight for adherence to the harvest prescription and intent of the harvest. When compared with the Lane Creek and MacKay Creek harvests *(fig. 1),* the Frog Heaven harvest was similar in that it produced more and shorter logs; however, the number, proportional representation, linear length, and tonnage of large logs retained was vastly different. For all these latter variables, the Frog Heaven harvest was significantly higher in the percentage change from the pre-harvest condition (all p-values <0.001 to 0.002). In part, this may have been a function of the greater proportion of large-diameter snags in the stand. It also suggests that if rigid standards of performance are demanded from a logging contractor that preservation of large, legacy logs is possible. One could argue that the greater tonnage of residual logs post-harvest at Frog Heaven constitutes a fuel hazard. However, their overall greater proportional representation and physical size makes them less likely to ignite and burn except in the hottest of fires; thus, for the time being, the intent of reducing fire hazard was met.

Case 4—Selection Harvest/Underburn in Ponderosa Pine

The number of all logs remaining after harvest and underburning in the Spring Creek and Grande Ronde ponderosa pine sites (192 and 72 logs per ha) *(table 5)* bracketed the 115 logs per ha observed in the largely unharvested ponderosa pine stands in the Five-Lock Demonstration area *(table 2).* Thus, in terms of the overall CWD component, (i.e., excluding the overstory that would provide recruitment for logs in the future), the Spring Creek and Grande Ronde harvest/underburn treatments approximated the relatively undisturbed, (i.e., not recently harvested), ponderosa pine stands in Case 1. The post-harvest/underburned Spring Creek and Grande Ronde stands easily exceeded the Standards for density of large, qualifying logs (20 and 25 logs vs. the Standard of 7-15 logs per ha) and for total lineal length (85 and 130 m vs. the Standard of 6-12 m per ha) *(tables 1, 5).* As a consequence of the greater mean length of logs in these harvested/underburned sites, total lineal length of logs was substantially greater (85 and 130 m per ha) than in the Five-Lock ponderosa stands (47 m per ha) (*tables 2* and *5*, respectively). This suggests that even after the imposition of selective harvest and underburning in the Spring Creek and Grande Ronde stands, post-treatment density of logs still exceeded those observed in the relatively unexploited Five-Lock Case, as stipulated in the Standards.

Table 5—*Log resources after selection harvest and underburning to favor ponderosa pine and western larch, and reduce encroachment by Douglas-fir and grand fir in northeastern Oregon. La Grande Ranger District, Wallowa-Whitman National Forest, Forest Service, U.S. Department of Agriculture, 1998.*

	Logs ≥ 15 cm in large-end diameter						Logs ≥ 30 cm LED[1]	Logs ≥30 cm SED[2]
Stand (year)	**Logs per ha**	**Percentage cover**	**m^3 per ha**	**Metric tons per ha**	**Total lineal length (m) per ha**	**Mean log length (m)**	**Logs per ha**	**Total lineal length (m) per ha**
Spring Creek (1998)	192	2.7	126	16	184	10.4	20	85
Grande Ronde (1998)	72	0.8	52	6	57	8.5	25	130

[1] large-end diameter
[2] small-end diameter

This Case contrasts with Cases 2 and 3 that resulted in shorter log lengths as a consequence of harvesting activity in mixed conifer stands. Specifically, pre-treatment vs. post-treatment lengths of logs in these ponderosa pine stands seemed to be less affected by harvesting than in those mixed conifer stands (*table 5* vs. *tables 3* and *4*). Presumably, the lower density of logs on the ground allowed harvesting equipment more options of going around rather than over logs, preventing breakage of residual logs.

Conclusions

Overall, it is difficult to assess the success of the salvage/fuel-reduction harvests. Post-harvest tonnage of CWD increased modestly, but presumably the remaining large standing dead trees, which were maintained for their value to wildlife structure, would ultimately contribute less to fuel-loading and hazard on the site than if the small standing-dead component (≤38 cm dbh) had been left to fall. The outcome of these salvage/fuel reduction harvests suggests that fuels were not reduced as much as one might intuitively think. However, the reduction in standing dead volume would represent a lesser fuel risk, and the crushing and breaking down of much of the CWD on the site would lead to fuels being in closer contact with the ground. The crushed fuels would be expected to remain moist longer into the fire season, and to decay more rapidly, minimizing fire risk and hazard for the near future.

A question that remains, however, is whether the residual stands in these four cases will continue to provide the targeted levels of log resources through recruitment of some of the residual trees that die and/or fall. The Decision Notice states that, "it is not the intention of this direction to leave standing trees for future logs in addition to the required snag numbers" (p. 11, Lowe 1995). Thus, it is possible for the Decision Notice Standards for logs to be met after harvest, but not have an adequate cohort of residual trees left to provide for future log resources. The concept of having a sustainable flow of resources, including CWD, is crucial to management, and should be addressed in future standards.

Determining if standards are being met after management prescriptions have been applied, or to otherwise quantify CWD, requires statistically valid and efficient sampling methods for this stratum. Bate and others (2002) present an alternative to the time-honored line-intercept inventory method of Brown (1974) for log sampling. Specifically, their alternative uses a time-saving strip-plot method for measuring density, percentage cover, total lineal length, weight, and volume of logs in stands and landscapes in interior northwest mixed-conifer stands. The method is also adapted to sampling in the lower log densities common in ponderosa pine stands.

Few inventories of log resources routinely use density as an expression of measurement (Bull and others 1995, 1997; Torgersen and Bull 1995), despite the fact that desired densities are stipulated in the Decision Notice Standards. Studies in wildlife ecology commonly use percentage cover to express log resources (Buchanan and others 1999, Carey and Johnson 1995, Carey and others 1999, Wilson and Carey 2000). This variable is also referred to as projected area or projected cover (Caza 1993, Harmon and Cromak 1987, Marshall and others 2000). Thus, for future standards that describe CWD, use of percentage cover (i.e. projected cover) would be a valuable descriptive parameter to include. Overall, for future inventories of CWD, sampling designs should supply information on density, percentage cover, and volume as minimum descriptive parameters for CWD $\geq$ 15 cm in large-end diameter. Furthermore, measuring large-end diameters as continuous variables—so that they can be categorized according to any desired diameter classes—is a valuable data set for managers.

The new information from these case studies suggests that the Decision Notice Standards, at least for mixed conifers and ponderosa pine, are attainable. But fundamental questions that still beg answers are "How much CWD is enough?" and "Are the Standards sufficiently high or too low?" Some newer published data partly address these questions. Based on the work of Bull and Holthausen (1993) and Torgersen and Bull (1995), for pileated woodpeckers at least, the Standards now appear too low! These data suggest that in pileated woodpecker home ranges the Standards are little more than half of what they could be in terms of pieces per unit area (59 to 77 per ha vs. 37 to 49 in the Standard). The piece-length Standard (> 2 m, with small-end diameter of 30 cm), regardless of management intent is only a third of what now seems appropriate. The concept in the Standards which stated that "longer logs may count for multiple 'pieces' without cutting them" (p. 11, Lowe 1995) recognized the value of long logs, but fell short of prescribing appropriately longer logs in sufficient numbers, largely because of the absence of appropriate data at the time. A mean piece-length standard of 6-9 m, for logs with a large-end diameter of $\geq$ 38 cm, is closer to observed log lengths in mixed conifer stands in northeastern Oregon, for example (Bate and others 2002, Bull and others 1997). Also, the large-end diameter is a more efficient parameter to estimate than the Standards' small end diameter of 30 cm somewhere along a log's length. New piece-length standards of 6-9 m would yield a new total lineal length standard approximating 300 to 600 m vs. the 30-43 m of the existing Standard.

The task of prescribing standards for how many, how big, and what kinds of logs to retain after management prescriptions is complex. It cannot be done without consideration for what there is in the residual standing living and dead components from which future CWD will be recruited over time. Having empirical data on CWD to incorporate into predictive models—and then using those models to formulate realistic, attainable standards—is crucial to sustainable forestry. As science and society become more knowledgeable about the complexities of ecosystems and their management, the collection and analysis of empirical data on CWD will be as important as it has been for living trees. Such inventories also need to be coordinated with the habitat needs for selected wildlife species of concern. This will mean support, both within the National Forest System and in research, for aggressive inventory programs that will provide data on CWD that measure up to the same statistical standards as for commodity resources.

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Sampling Methods for Snags and Large Trees Important to Wildlife[1]

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Abstract

We developed efficient and accurate methods for sampling snags and large trees important to wildlife. These methods are described in detail in a recent Forest Service publication, which also includes spreadsheets, macros, and instructions to conduct surveys and analyses to estimate densities and distributions of snags and large trees on a landscape. These methods focus on optimizing sampling effort by choosing a plot size appropriate for specific forest conditions encountered. Two methods for assessing density are available. Method I requires sampling until a desired precision is obtained for a density estimate. Method II is designed to test for differences in observed snag density versus a desired target density. After collecting a minimum of 60 samples under method II, one may test for a significant difference between the observed and targeted densities. In addition, data can be used to calculate a distribution index. The value obtained from the distribution index helps managers assess whether the current distribution of snags and large trees across a subwatershed is adequate to meet the habitat needs of territorial cavity-nesters and other wildlife species. Wildlife use of snags and large trees may also be evaluated.

Introduction

Snags and large trees are important to a wide variety of wildlife species for survival and reproduction. (Bull and others 1997, Thomas and others 1979). Woodpeckers are an especially important group of species that rely on a continuous supply of snags and large trees. As primary cavity-excavators, woodpeckers create the cavities within snags or trees that they and a myriad of other species use as nest and roost sites. In turn, these same cavities also provide thermal and hiding cover for many resident wildlife species during the non-breeding season.

National Forests are required by law to maintain viable populations of all native wildlife species (Forest and Rangeland Renewable Resources Planning Act 1974). Specifically, National Forests are required to monitor native species or their habitat to ensure the presence of viable populations through maintenance of well-distributed habitats throughout the planning area (U.S. Laws, National Forest Management Act

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1976). Because woodpeckers play an integral role in forested ecosystems, they have been a primary focal species for monitoring efforts on National Forests (Bull and others 1991).

Monitoring requires considerable time and money. Consequently, if resource specialists are to monitor habitat for woodpeckers and other cavity-nesters accurately, these specialists need efficient and statistically valid sampling methods. In response to this need, we produced a Forest Service General Technical Report (GTR) as a guide for resource specialists in the sampling and monitoring of snags and large trees. Included in the report (Bate and others 1999) are the spreadsheets, macros, and instructions needed to conduct all surveys and analyses pertaining to the estimation of snag and large tree densities, and their distributions on a landscape.

This paper highlights the essential considerations for sampling snags and large trees on a landscape as a companion to the earlier GTR of Bate and others (1999). Specifically, this paper was written to facilitate a better understanding of the methods required for accurate estimation of snag and large tree density and distribution, in support of monitoring efforts for cavity-nesting birds on National Forests. Improvement in the understanding of these methods and their accuracy is particularly important in light of findings that indicate failure of National Forest management to provide adequate densities of snags and large trees for cavity-nesters (Bate 1995, Morrison and others 1986).

Key Considerations for Sampling Snags and Large Trees

Before beginning a sampling program for snags or large trees, resource specialists must first make two key decisions about plots: plot shape and size. In general, long, narrow or rectangular plots work better than circular or square plots (Krebs 1989). This is because the habitat components of a forest are never uniformly distributed; rather, habitat components such as snags tend to occur in clumps or patches. Consequently, rectangular plots are better for sampling because they cross through more clumps of snags or trees, rather than encircling, or missing clumps completely. The outcome is a lowered variance, which translates into smaller sample sizes. Rectangular plots, therefore, are recognized as the optimal plot shape for sampling in patchy habitats (Krebs 1989) and are the shape that we recommend.

The second decision, relating to what size of plot to use, is not readily discernible. This is because no single plot size is optimal for all forested conditions. We define the optimal plot size as that which minimizes sampling effort while maintaining accuracy and precision. Each forest situation must be analyzed independently, because the optimal plot size depends on a number of factors such as density and distribution of snags or large trees, topography, seral stage, and amounts of downed wood or shrub cover.

Analysis for Optimal Plot and Sample Size

Sometimes a plot size can be selected based on knowledge of the area, but in many forested areas the optimal plot size for sampling snags or large trees is unknown until a pilot sample is conducted. A pilot sample provides an initial estimate of the density of snags or trees likely to exist in a given area. A pilot sample also provides information about the distribution of snags or trees. Information from the pilot survey can be used in two specific ways with the spreadsheets found in Bate and others (1999): to identify optimal plot size and to calculate the number of samples needed to obtain a desired level of precision.

Eight plot sizes are available for use within the spreadsheets provided by Bate and others (1999). As part of the pilot sample, field observers record the perpendicular distance to a snag or large tree from the centerline of the transect. Based on these distances, a macro within the spreadsheets truncates the number of snags or trees in 5-meter intervals. This allows the user to estimate the density and variance of snags for each of the eight plot sizes. Subsequently, this information is used in the spreadsheets in a variety of ways. First, the spreadsheet calculates the total number of plots and hectares required for sampling with each plot size. Secondly, this information is combined with a cost factor to help determine which plot size is optimal based on the given forest conditions.

Cost seems to be a function of three factors: visibility, terrain, and density. Limited visibility owing to the seral stage or dense shrub cover within a stand can increase search time for snags, and therefore cost, if too wide of a plot is used for sampling. Too wide of a plot can also lead to biased estimates of density. Similarly, if field conditions are difficult for an observer to travel through, or a consistently high number of snags or large trees (>15 per plot) are encountered within each plot, a narrower plot width is likely a better choice. The optimal plot size is that which minimizes sampling effort while maintaining accuracy and precision.

Stratification

When sampling on a landscape scale of a subwatershed or watershed, it will be rare that forest conditions will be similar throughout such large areas. Consequently, stratification is critical in reducing variance, and in turn, reducing sampling intensity needed to meet sampling goals. As a result, Bate and others (1999) provide a high level of detail about effective methods of stratification or the creation of homogeneous forest categories to reduce sample size requirements. To guide the stratification process, Bate and others (1999) include a spreadsheet called “Sample Size.” This spreadsheet calculates the sample size required and how the samples should be allocated by stratum (homogeneous categories). Two allocation methods are provided: a proportional method and optimal method. The proportional method allocates samples among strata based on the proportion of the area within each stratum. In contrast, the optimal allocation method incorporates both the proportion of the total area and the variance of each stratum. There are advantages and disadvantages to both approaches (Bate and others 1999).

Density Analyses

Two options for obtaining a density estimate are available. Under the first option, a sufficient number of samples are collected to obtain a desired level of precision (e.g., within 20 percent of the true mean 90 percent of the time). In areas where snag densities are high and not severely clumped, obtaining a density estimate within a desired precision usually can be done with a reasonable amount of effort. In areas that have been intensively harvested and few snags have been retained, however, the number of samples required (in hectares) to obtain a desired precision can exceed the land area available. Consequently, Bate and others (1999) provide a second density analysis option, which is a straightforward statistical test to compare estimated densities with targeted densities. For example, is the density estimate of snags different from the Forest Plan standards, which requires five snags per hectare? One great advantage of this method is that the test can be conducted after a minimum of 60 samples has been collected.

Further Analyses

Another feature of the Bate and others (1999) GTR and its spreadsheets is the method presented for calculating a distribution index. The distribution index helps managers assess whether the current distribution of target snags and large trees across a subwatershed is adequate to meet the habitat needs of territorial cavity-nesters and other wildlife species. The distribution index is a useful complement to the estimation of snag density because small areas of subwatersheds sometimes contain a major proportion of all snags in the subwatershed, rendering most snags as unavailable to territorial species. Thus, application of the distribution index gives managers appropriate insight about how well their snag density goals can be met from the standpoint of distribution.

For resource specialists interested in more than density or distribution, the spreadsheets also offer an algorithm to calculate nesting use. This algorithm is given as a percent use value and can also be applied to calculate foraging use.

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Accuracy and Efficiency of Methods to Sample Logs for Wildlife Research and Management[1]

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Abstract

We evaluated performance (accuracy and efficiency) of the line-intersect and strip-plot methods for estimating the density, length, percent cover, and weight of logs important to wildlife. To conduct the evaluation, we sampled 17 coniferous stands in northeastern Oregon and northwestern Montana. These stands contained a gradient of log conditions based on seral stage, physiography, disturbance regime, and history of timber management. A complete count (census) of logs in these stands was used to evaluate the precision, bias, and efficiency of each sampling method. Preliminary results indicated that both methods were relatively unbiased and precise. The strip-plot method, however, was more efficient in estimating density, but neither the strip-plot method nor line-intersect method was clearly more efficient in estimating length, percent cover, or weight. Consequently, which method is better depends on a variety of factors, particularly the stand conditions to be sampled and the log characteristics of most interest. Our results also demonstrated the strong difference in methods needed to sample logs for wildlife research and management versus conventional methods that have been used for fire management.

Introduction

Fallen trees, often referred to as logs or coarse woody debris, are a critical resource for a myriad of wildlife (Maser and others 1979). Logs act as a foraging substrate and a food base for a variety of birds and mammals (Carey and Johnson 1995, Tallmon and Mills 1994, Torgersen and Bull 1995). Logs also function as thermal and hiding cover for many reptiles, amphibians, and mammals (Maser and others 1979, Parks and others 1997). Moreover, large hollow logs serve as den, hibernation, and shelter sites for black bear *(Ursus americana),* American marten *(Martes americana),* and a variety of small mammals (Parks and others 1997).

Despite the importance of logs to survival of wildlife, little work has been done to develop and test methods to sample logs from the perspective of meeting wildlife

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needs. Brown (1974) adapted the line-intersect method (LIM) to estimate the volume and weight of logs for managing fuels and predicting fire behavior. Brown's sampling method was based on the line-intersect technique developed by Van Wagner (1968), who evaluated the technique using matchsticks of equal length and diameter. Hazard and Pickford (1986) further evaluated Van Wagner's line-intersect method using computer-simulated log populations; simulations were drawn from a population of logs that were tapered and variable in length, based on data collected from stands that were clearcut. Hazard and Pickford (1986) found that the sampling effort needed to achieve the same precision as that in Van Wagner's (1968) study increased sixfold when logs of variable length and shape were used. Hazard and Pickford (1986), however, verified that the LIM produced unbiased estimates of coarse woody debris when sampled using random location and orientation of line transects.

Because the LIM was developed to estimate log characteristics important for fuel management, namely volume and weight, not all structural characteristics important to log-dependent wildlife are measured with conventional application of this method. For example, percent cover of logs, which is not measured for purposes of fuel management, was correlated positively with the abundance of small vertebrates and their forage base in recent studies (Carey and Johnson 1995, Tallmon and Mills 1994). Log density, large-end diameter, and length, none of which are outputs of Brown's line-intersect method, were documented as important variables in defining foraging habitat for the pileated woodpecker *(Dryocopus pileatus)* (Bull and Holthausen 1993, Torgersen and Bull 1995).

In this paper, we describe procedures and preliminary results for testing the performance of two sampling methods to estimate the density, length, percent cover, and weight of logs considered valuable to wildlife. Specifically, we compare two approaches: the line-intersect (Brown 1974, DeVries 1973) and strip-plot methods. We compare each method in terms of precision, bias, and efficiency under a variety of field conditions.

Study Area

Seventeen coniferous stands in the Blue Mountains of Oregon and the Salish and Mission Mountains of Montana were selected for sampling. Our main objective in selecting stands was to sample a gradient of log densities, lengths, percent cover, and weights representing a range of conditions found within the Columbia River basin east of the Cascade Mountains. These variable conditions were a function of seral stage, shrub abundance, slope, disturbance regime, and history of timber management.

Nine of the 17 stands were unharvested, which we defined as stands composed primarily (≥90 percent) of logs whose lengths had not been altered by timber harvest or gathering of fuelwood. Unharvested stands typically had closed canopies and were in mid- or late-seral stages of development. The other eight stands, referred to as harvested, had a history of more intensive timber management; clearcutting and seed-tree cutting occurred in these stands within the last 10 years.

Stand size averaged 3.3 ha and ranged from 1.2 to 7.4 ha. Slopes ranged from 0 to 85 percent. Grand fir *(Abies grandis),* western larch *(Larix occindentalis),* lodgepole pine *(Pinus contorta),* Douglas-Fir *(Pseudotsuga menziesii),* and ponderosa pine *(Pinus ponderosa)* dominated one or more stands in Oregon. Stands in Montana were dominated by two or more of the following: western larch, Douglas-Fir, grand fir, lodgepole pine, Engelmann Spruce *(Picea engelmannii),* subalpine fir *(Abies lasiocarpa),* and white pine *(Pinus monticola).*

Methods

Field Procedures

To evaluate our sampling methods against known parameters, within each stand we first conducted a complete count (census) of all logs that had a large-end diameter of 15 cm or greater and a length of at least 1 meter. Trees that had fallen and broken were tallied as two pieces if the pieces were not touching; otherwise, each fallen tree was considered one piece. Only logs whose central axis lay above the ground were tallied (Brown 1974). If a log was suspended, only that portion of a log that was within 1.8 meters of the ground was tallied. A log was considered downed if it lay within 45 degrees of the ground. In the remainder of this paper, we refer to logs of these dimensions and characteristics as "qualifying" logs.

Each log was painted at both its large and small ends where the diameter measurements were taken using 1 m-long calipers. Diameters were measured to the nearest millimeter. Lengths of logs were measured to the nearest decimeter between the painted diameter marks. For large logs with their root systems still attached, the large-end diameter was measured just above the butt swell, whereas the length was measured along the entire bole from the root wad out to the 2-cm small-end diameter.

After finishing the complete count of logs, we then sampled along randomly established transects. We established six transects in most stands. Because of size constraints, however, a few stands only contained five transects. All transects were randomly located and oriented to minimize overlap. The typical transect was 100 m long and was delineated into 12.5 m subsegments; some stands, however, contained shorter transects owing to limitations on stand size. At the midpoint of each transect we established a cluster unit. This was a three-legged sampling unit, with each leg 25 m long and oriented at 120 degrees from other legs. Design of the three-legged sampling unit followed the example given by Hazard and Pickford (1986).

We then sampled along each 12.5 m subsegment using both the line-intersect method (LIM) and the strip-plot method (SPM). For the SPM, we conducted a complete count of all logs, or portions of qualifying logs, that fell within 2 m of either side of the transect line. We used the 1-m long calipers, which by design functioned as a square, to determine the outer boundaries of the strip plots. By contrast, only logs that were intersected by the transect line were tallied using the LIM. For the SPM, we recorded the length, the small- and large-end diameters, and the condition (sound or rotten) of each section of a qualifying log that fell within the boundaries of the strip plot. In addition, we recorded whether or not the mid-point of a log fell within the boundaries of the plot. For the LIM, we recorded the same information as with the SPM. In addition, we recorded the diameter of the log at the point of intersection.

Statistical Analysis

We used ordinary least squares regression to examine the relation between the true values of log density, total length, percent cover, and weight in each stand compared to our estimates of these parameters obtained from the SPM and the LIM. Specifically, we regressed the true value of log density, total length, percent cover, and weight on the estimated values generated by LIM and SPM. This resulted in four regression equations for each method, with one equation corresponding to each of the four log characteristics of interest. For the preliminary analysis conducted here, we used data from all stands to compute each equation, with each stand designated as a statistical unit of observation (n=17).

To evaluate bias of each method, we forced each regression line through zero by removing the y-intersect constant. This allowed us to determine whether a method over- or underestimated each parameter. Specifically, a regression slope (b) = 1.0 indicated no bias. By contrast, $b > 1.0$ indicated that the sampling method underestimated the true parameter, whereas $b < 1.0$ indicated that the sampling method overestimated the parameter.

To evaluate precision of each method, we used the coefficient of determination (r^2 values) obtained from the regression analysis. Coefficients of determination at or near 1.00 (100 percent) indicated high precision, whereas coefficients at or near 0.00 (0 percent) indicated extremely low precision.

To evaluate efficiency, we used two approaches. Under the first approach, we calculated the length of transect line required for each method to obtain an estimate of each log characteristic that was within 20 percent of the true mean, 90 percent of the time. Sample sizes given were based on the average length of transect required per stand. We standardized these calculations by using only straight-line transects that were 100 m long (n=75). We then incorporated the true value for each parameter obtained from our complete counts, rather than the sample value, into the sample size equation. This controlled for any strong influences created by using the sample mean statistic.

Under the second approach, we ranked the amount of field time (sampling effort) that was required by each method to measure each of the four log characteristics. Ranks were assigned on a relative scale that ranged from 1 to 3, as follows: rank 1, least effort; rank 2, moderate effort; and rank 3, most effort.

Results

Accuracy

Both the LIM and SPM produced relatively unbiased estimates of density, length, percent cover, and weight of logs. Values of b ranged from 0.99 to 1.04 for the LIM and from 0.97 to 1.02 for the SPM. Precisions of these estimates, however, were more divergent between the two methods. Coefficients of determination ranged from 0.58 to 0.93 for the LIM and from 0.75 to 0.94 for the SPM. In particular, the LIM was relatively imprecise in estimating density of logs, accounting for only 58 percent (0.58) of the variation in the true density. By contrast, the SPM accounted for 75 percent of the variation in the true density of logs. Finally, precision of both methods in estimating length, percent cover, and weight was relatively high, with coefficients of determination ≥ 0.82.

Efficiency

The LIM required more transect length per stand than the SPM to achieve the same level of precision for estimating density, length, percent cover, and weight of logs under all stand conditions. Transect length required of the LIM ranged from 1.0 to 3.8 km, while transect length required of the SPM ranged from 0.7 to 1.8 km. Differences were most pronounced for estimates of weight in harvested stands, where the LIM required an average of 138 percent more transect line per stand (3.8 km) compared to the SPM (1.6 km) to obtain the same level of precision.

Field effort required of LIM also was greater (ranking of 3) than SPM (ranking of 1) for estimating density of logs. The LIM required less field effort, however, than the SPM to estimate length and weight (LIM rankings of 1 versus SPM rankings of 2). Finally, either less field effort or the same amount of effort was required using LIM versus SPM to estimate percent cover, depending on how log diameters were measured with LIM. When large- and small-end diameters of logs were measured as part of the estimation of percent cover under LIM, field effort was ranked as moderate, the same as that estimated for SPM. Alternatively, when log diameters were measured at the point of line intersection under LIM, field effort for estimating percent cover with LIM was ranked as low.

Discussion

Our results indicate that both the LIM and SPM are relatively unbiased and precise estimators of most log characteristics under the conditions tested. The SPM appeared to be more precise, however than LIM in estimating density of logs. SPM also was more efficient than LIM in estimating density. By contrast, neither SPM nor LIM was clearly more efficient in estimating length, percent cover, or weight of logs. Consequently, which method is better depends on a variety of factors, particularly the stand conditions to be sampled and the log characteristics of most interest. For example, if the primary interest is to obtain accurate, efficient estimates of log density, then SPM appears to be the better choice. If other log characteristics are of primary interest, the choice of method is less clear. Finally, if all four log characteristics are of equal interest, SPM is the likely choice owing to its superior performance in estimating log density. We are currently exploring questions about each method's performance in relation to a variety of field conditions, using additional data collected during our study. Further analysis of our data should help clarify the merits of each method under a variety of conditions.

Our results also demonstrated the strong need for different methods to sample logs for wildlife research and management versus conventional methods that have been used for fire management. Conventional applications of LIM for fire management estimate log volume and weight, but ignore density, percent cover, and length. Because wildlife respond to a rich set of log characteristics, it behooves wildlife managers and researchers to apply methods like those described here to obtain accurate estimates of log characteristics most important to wildlife.

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Effects of Prescribed Fire in Ponderosa Pine on Key Wildlife Habitat Components: Preliminary Results and a Method for Monitoring[1]

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Abstract
We monitored the effects of prescribed fire in ponderosa pine forest on snags, down logs, oaks, and old ponderosa pine trees. Five prescribed burns were monitored over a total of 47.7 ha (118 acres). The prescribed fires consumed more than 50 percent of the 342 down logs and approximately 20 percent of the 138 snags monitored. The fires created few snags or down logs. Our methodology evolved from a variable plot method to a grid method through a series of sites. The final method—using a grid, aluminum tags, and sketch mapping—resulted in almost a 50 percent time saving at the end of the first post-burn reading.

Introduction

The reintroduction of fire into the current forests has the potential to greatly change the frequency and distribution of key wildlife habitat components, such as snags, down logs, old trees, and large oaks *(Quercus gambeli).* Snags are an important habitat component and need to be present at appropriate densities in forested ecosystems for cavity nesting birds (Cunningham and others 1980, Horton and Mannan 1988, Newton 1994). Down logs are important to small mammals and need to be well distributed across the landscape to provide for wildlife habitat (Goodwin and Hungerford 1979). Oaks provide key habitat for wildlife in the Southwest, including birds, bats, ungulates and small mammals. Oaks are one of the most important factors affecting bird distribution (Rosenstock 1998) in northern Arizona ponderosa pine *(Pinus ponderosa)* forests. Old-growth ponderosa pine trees are used by 80 species of wildlife on the Coconino National Forest for nesting, feeding, foraging, and roosting sites.

Forest managers in the Southwest use prescribed fire to restore the health of ponderosa pine ecosystems and reduce the threat of catastrophic wildfire. Prescribed fire has become more important recently because of increased emphasis on forest restoration, urban interface fire prevention, and fire as a vegetation management tool.

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Little published information is available, however, on the effects of prescribed fire on snags, logs, oaks, and old-growth ponderosa pine trees.

Since 1995, we have been monitoring prescribed fire on two national forests and a national monument to determine effects on selected wildlife habitat components. These data are intended to give resource managers better information about gains and losses of key wildlife habitat components following prescribed fire in northern Arizona. This paper presents data from five burns. Our study is ongoing and eventually will include 10 sites. The data we have collected to date provides needed information on the effect of prescribed fire on key wildlife habitat components in ponderosa pine forests.

The prescribed burns we have studied are the first use of prescribed fire on each site. The results represent effects of the first entry with prescribed fire, which may cause the most change to wildlife habitat depending on the frequency of reentry burns.

Study Area and Methods

We monitored pre and post-burn habitat components on five sites totaling 47.7 ha (118 acres). The sites are located near Flagstaff in north central Arizona. The five sites include three ranger districts on the Coconino National Forest, one ranger district on the Kaibab National Forest, and Walnut Canyon National Monument. The sites are named Walnut, Unknown, Stoneman, Twin Springs and Howard.

All the sites are in the ponderosa pine vegetation type *(table 1).* Some of the sites also include varying proportions of Gambel oak and alligator juniper *(Juniperus deppeana).*

Table 1—*Pre-burn habitat component data by site.*

	Number of components/ha (components/acre)					
Site	**Snags**	**Logs**	**Oaks**	**Old-growth trees**	**Ha monitored**	**Habitat type**
Walnut	6.1 (2.5)	6.1 (2.5)	>1	19.8 (8.0)	8.9 (22)	Ponderosa pine
Unknown	1.5 (.6)	3.7 (1.5)	>1	26.7 (10.8)	14.2 (35)	Ponderosa pine
Stoneman	1.9 (.77)	7.9 (3.2)	8.4 (3.4)	5.4 (2.18)	8.9 (22)	Ponderosa pine/Gambel oak
Twin Springs	3.2 (1.3)	9.4 (3.8)	6.8 (2.8)	11.3 (4.6)	9.7 (24)	Ponderosa pine/Gambel oak
Howard	6.6 (2.7)	13 (5.3)	22 (8.9)	3 (1.2)	6.0 (15)	Ponderosa pine/Gambel oak

All the monitoring sites on the national forests have similar histories, with logging beginning in the late 1800s and continuing until the present decade. Recent logging includes both pre-commercial thinning of trees less than 5 inches (12.7 cm) dbh, and varying levels of overstory removal. Wildfire suppression began in the early 1900s.

The Walnut Canyon National Monument site is strikingly different because it has never been logged, although wildfire suppression history is similar. The Walnut site has a substantial old-growth ponderosa pine component and is structurally diverse.

The sites are approximately 6 to 14 ha (15 to 35 acres) in size depending on the density of habitat components. On each site, we attempted to monitor an area large enough to include at least 50 individuals of each component studied. This number was selected to try to balance biological significance and data collection practicability. In practice, some sites did not achieve the desired number of all habitat components. Snags proved to be the most rare component, and none of the sites burned so far contained 50 snags. In each instance, we truncated the sites to keep their size manageable or to remain within the prescribed fire area. One site (Howard) also failed to meet the desired number of old ponderosa pine.

Prescribed Fire

Sites are located within prescribed burns planned in the normal course of forest management. The burn prescriptions followed normal agency practice. Sites selected are in areas where agency personnel had planned prescribed burning. We made an effort to find burns carried out by a variety of crews in order to assess variability caused by crews as well as sites.

All five burns monitored occurred in the fall. Prescribed fire burning plans were similar for all burns conducted *(table 2)*. Fuel moisture in the 1,000-hour fuels ranged from 13 to 16 percent. Firing techniques and devices were the same for all burns. Planned weather conditions and general topography of all sites were similar.

Table 2—*Prescribed fire data and monitoring dates.*

Site	1,000-hour fuel moisture percent	Firing techniques	Humidity percent	Temperature (degrees F)	Month/year burned	Post-burn data	Post-burn year 3	Post-burn year 6	Post-burn year 10
Walnut	15	Head and Backing			10/96	6/97	6/00	6/03	6/06
Unknown	12	Head and Backing	15 –60	75	12/95	6/96	6/99	6/02	6/05
Stoneman	16-50	Head and Backing	15-100	40-80	9/97	10/97	6/01	6/04	6/07
Twin Springs	15-32	Head and Backing	20-60	40-75	10/97	10/97	6/01	6/04	6/07
Howard	15-50	Head and Backing	15-100	40-80	9/97	10/97	6/01	6/04	6/07

We surveyed sites prior to the prescribed burn and within 1 to 11 months after the burn *(table 2).* Sites will be surveyed again at 3, 6 and 10 years after the burn. These follow-up surveys are intended to capture changes such as tree mortality, which may be delayed for several years after the burn that caused it.

Component Data Collection

We surveyed all the individual habitat components on each site. DBH and height were recorded for mature ponderosa pine, oaks, and snags. Down logs were characterized by species, minimum diameter, maximum diameter, and length. Compass bearing from largest end of the log and whether the tree was cut or fallen was recorded. The compass bearing assisted us in identifying the log after the burn. Additional data collected on each component included presence/absence of leaves, twigs, bark, cracks, cavities, litter depths, and animal usage for later analysis.

Changes in Data Collection

As we began study design, we considered a variety of sampling methods. Difficulties in estimating the extent of change with rare components led us to believe the best method would be a total count of habitat components within known area sites. Although we have consistently conducted a total survey of habitat components on the sites, the methodology for conducting the total survey has changed as we have learned from the post-burn sites.

Variable Plot Method—Few Tags

When we began the project, we based surveys on groups of ponderosa pine. The location of a central point in each ponderosa pine group was recorded by using a global positioning system (GPS), and one or more trees were marked with an aluminum tag bearing a group number. One point consisted of either a single component or multiple components, i.e., GPS point R080813A recorded presence of two down logs and both were tagged with the identifier number. A map of all points was produced, showing the relationships of the points to each other on the ground. Points were easily relocated; however, because the size of points varied, one could not quickly summarize which habitat components were within the point without checking tags.

Variable Plot—All Items Tagged

The first change we made was to begin tagging all the habitat components with aluminum tags, which identified the components associated with the group central point. Although some tags melted in the burns, the tagging reduced the total time needed for post-burn data collection *(table 3).* Tagging all the components increased the time needed to set up a site by 2 person-days; however, tagging reduced the time needed for post-burn monitoring from 14 person-days to 8 person-days.

We continued to have some confusion on the edges of groups, since often a tree or a log could logically be recorded in either of two groups.

Table 3—*Person-days required for monitoring a plot through the first post-burn reading by method.*

Method	Setup	Post-burn	Total
Variable plot—few tags	8	14	22
Variable plot—all items tagged	10	8	18
Grid—all items tagged	10	2	12

Grid—All Items Tagged

Post-burn monitoring at Walnut revealed that a better method was needed. We could reconstruct some, but not all the groups from our data. It sometimes was very time consuming to reconstruct groups, particularly if a group was greatly changed by the burn. Since this was our most complex site, the problems with our methods were amplified. Because we could not reconstruct all of the groups at Walnut, the post-burn data for that site were truncated to include only data from the groups that could be reconstructed with certainty.

The difficult and time-consuming nature of the post-burn monitoring at Walnut led us to change our methods. We avoided using a grid at first because we thought it would take more time. After experience with the other two methods, we realized that laying out a grid could greatly reduce the time needed to read sites after a burn. We began laying out grid cells 30.48 m (100 feet) on each side, and continued tagging all the habitat components. Grid cell corners were marked with tagged rebar stakes. Each 929 sq. m. (10,000 sq. ft.) cell was issued a number. Grid cells were numbered so that each cell could be identified by unique alphanumeric code. All habitat components were tagged, sketched, and characteristics summarized by cell.

The final improvement made was a sketch map of each grid cell showing where the habitat components were in relation to each other within the cell boundary. The net effect of these changes was a dramatic decrease in the time needed to monitor a site post burn *(table 3).*

Results

Pre-burn—Site Habitat Description

Table 1 shows the pre-burn density of each habitat component for each site we monitored. Structural complexity (dog hair thickets, varying diameter of ponderosa pine) was low on the Howard and Unknown sites and moderate on the Stoneman and Twin Springs sites. The Walnut site is a very complex site with not only an abundance of old-growth, but also dog hair thickets and multiple age classes present.

Snags

We sampled 138 snags > 15 inches (38 cm) dbh, almost all of which were either ponderosa pine (87 percent) or Gambel oak (10 percent).

At all sites except Walnut Canyon, some snags were lined, i.e., duff and debris moved away from the base of snag. Snag lining was a common practice on all USDA Forest Service burns.

Twenty-nine snags (21 percent of all snags) were consumed by fire or converted to logs. The individual sites did not differ significantly in numbers of snags lost *(fig. 1).* The range of snag loss was 12-38 percent. Nine snags were created. Snags created by the prescribed fires were created predominately (six of the nine snags) at Walnut Canyon National Monument where old-growth trees were converted to snags. Two oaks, one each from the Howard and Twin Springs site, became snags. Average diameter for the snags gained are larger than the average pre-burn snag diameter.

Fourteen Gambel oak snags were included in the data. In the post-burn condition, 8 of the 14 oak snags remained. Initial results suggest that oak snags might be at higher risk of loss from prescribed burns than ponderosa pine snags. The additional sites that have not yet been burned will increase our sample size. Oak snags, however, are also extremely rare on these landscapes.

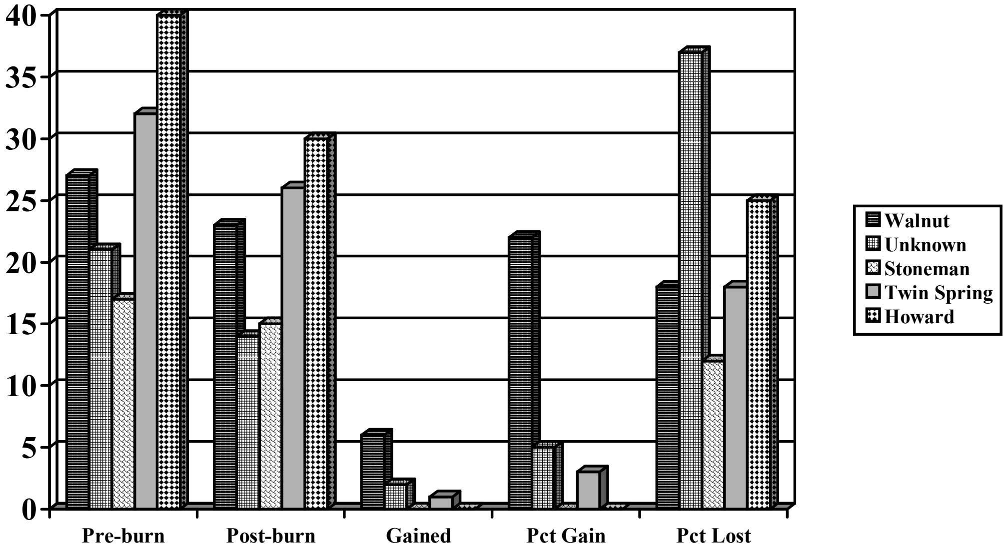

Figure 1—Snag data by site.

Logs

We sampled 342 logs > 15 inches (38 cm) dbh. Logs varied in diameter, length, decay condition, and use. Ponderosa pine, Gambel oak, and juniper represented 90.24, 7.38, and 2.38 percent, respectively, of the sample logs.

Fifty-three percent of all logs were lost. Log loss did not differ greatly by species. The range of log loss was 36-61 percent *(fig. 2)*. The prescribed burns created 15 logs. New logs created are located predominantly at Walnut Canyon National Monument (13 of the 15 logs) where conversions from old-growth tree to log and from snag to log were nearly equal. Average diameter and lengths for logs lost and created were very similar. Logs remaining in the post-fire condition were slightly smaller in diameter and 5 feet (1.5 m) longer based on the average of all logs monitored.

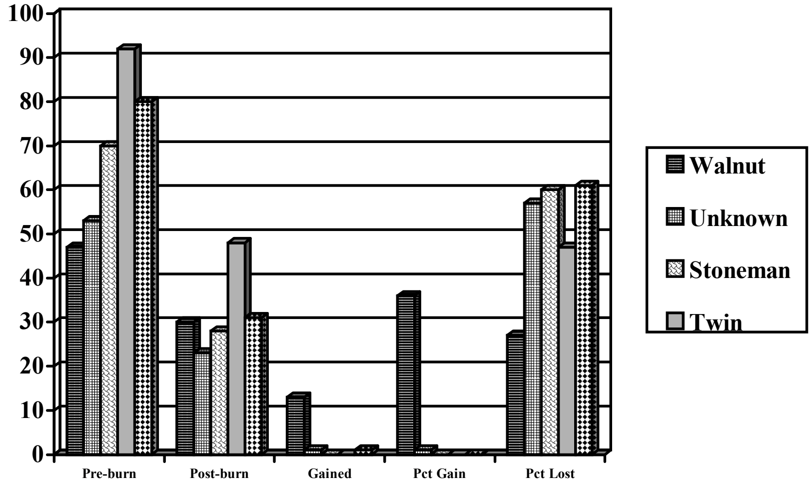

Figure 2—Log data by site.

Oaks

We sampled 282 oaks >10 inches (25.4 cm) dbh. All of our sites had oaks on them, but most oaks were on the three sites considered ponderosa pine/Gambel oak cover types (Howard, Twin Springs, and Stoneman). Both the Walnut and Unknown site recorded a few oaks.

Six percent of the total oaks were lost. The range of oak loss on the ponderosa pine/Gambel oak cover types was 0-9 percent *(fig. 3)*. The one oak at Unknown went unscathed; however, two of three oaks on the Walnut burn were killed. The third oak was charred badly. The three oaks on Walnut Canyon National Monument site were not in a clump; however, all three were adjacent to dog hair thickets where the fire got rather hot.

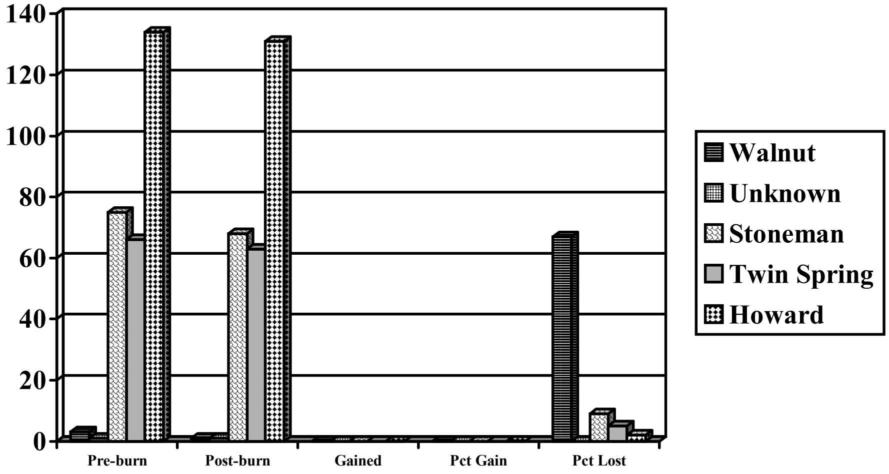

Figure 3—Oak data by site.

Mean diameter of oaks lost, 40.1 cm (15.8 in.), was slightly higher than the average pre-burn diameter (36.1 cm./14.2 inches). The possibility of delayed oak mortality and conversion of live oak to snag is one of the reasons for planning a 10-year monitoring effort.

Old-growth Ponderosa Pines

We sampled 680 old-growth trees on the five sites. The Walnut site contained a lower number of old-growth trees because of a site selection decision. The crew who set up Walnut avoided large clumps of old trees that did not contain other components in order to increase the sample size of the more rare habitat components.

Immediate post-burn monitoring found that few old-growth trees had died during or immediately after the prescribed fires *(fig. 4)*. Most of the trees that did die were on the Walnut Canyon National Monument site. The affected trees are now either snags or logs, and resulted in gains in the log and snag components. Old growth tree loss across the sites ranged from 0 to 6 percent.

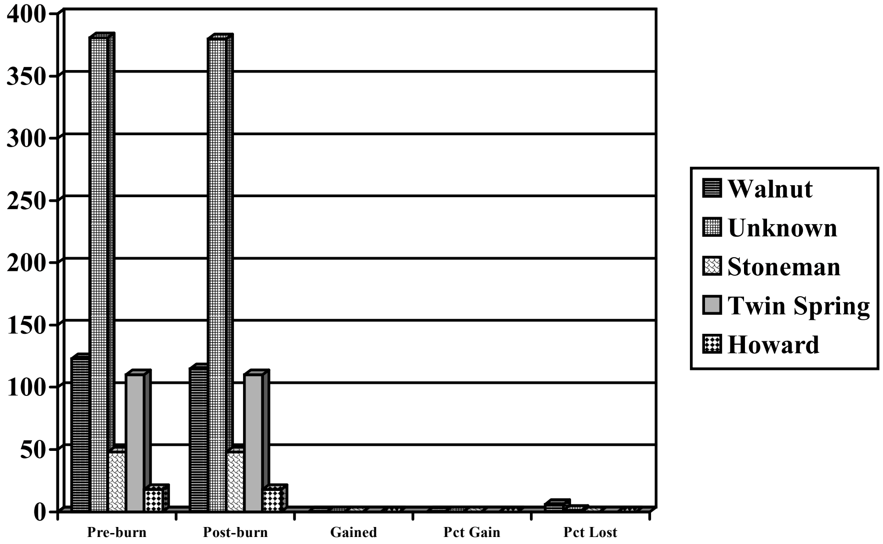

Figure 4—Old-growth pine data by site.

Survey Methods

Because the time saved by using the grid method will occur each time a site is monitored post-burn, the difference in the total time required for each sampling method will increase with the second and third post-burn reading. By the end of the project, after four post-burn readings of each site, we would have 64 person-days invested in a site using our original method, compared with 18 person-days with the grid method *(table 3)*.

Because most monitoring efforts will not require the detailed data we are collecting on each habitat item, our recommendation for future monitoring is to use a grid, tag each item, and use sketch maps of each cell. The pre-burn setup time without the detailed data on each item should be about half of what we have estimated. Post-burn site monitoring time is cut by about 25 percent without the detailed data collection. We would estimate reducing the total time for setting up a site and monitoring it twice to be approximately 8 person-days, or if the site is monitored four times after the burn, 11 person-days. Two post-burn measurements may well be enough, after the delay between the burn and tree mortality rates are well understood.

Discussion

Our monitoring has attempted to determine the effect of prescribed fire on wildlife habitat components. Our preliminary monitoring findings represent what we would expect to happen when conducting a fall prescribed fire where average 1,000-hour fuel moistures are approximately 15 percent. Our preliminary results describe the effects of prescribed burning in the fall in managed ponderosa pine stands with a sparse or scattered overstory of old trees. Under these prescribed burning conditions, our results show about 50 percent of the logs and about 20 percent of snags being consumed with little or no immediate gains *(fig. 5)*. Live oaks have been reduced by 6 percent and little immediate mortality of large old-growth ponderosa pines has occurred.

Recent forest management direction in the southwestern U.S. for snags and logs has come primarily through plans for the Mexican spotted owl and northern goshawk. These management plans recommend the use of prescribed fire to protect habitat from catastrophic wildfire and to improve understory vegetation (grasses, shrubs, forbs, wildflowers) beneficial to prey species for these raptors.

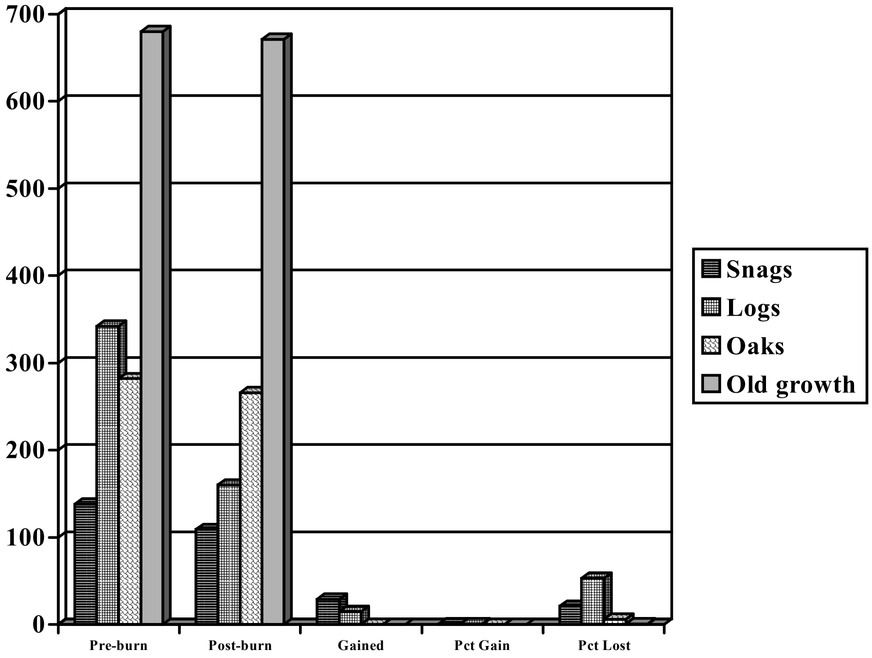

Figure 5—Habitat component data from five sites combined.

Horton and Mannan (1988) found that nearly half of all snags burned down, logs decreased by 42 percent and 56 percent, and prescribed fires in southeastern Arizona killed few large trees. Snags greater that 50 cm dbh were most impacted.

In a recent study of snag abundance, Ganey (1999) found that Forest Service snag standards were seldom met, even in unlogged forests. Our preliminary findings as well as these studies, suggest that densities of snags are often below those required by Forest Service guidelines and will be reduced further by the use of prescribed fire. Our initial results would suggest that oak snags might be at higher risk from prescribed burns than ponderosa pine snags. Our results to date are inconclusive; however, we have shown that fire kills some oak trees. On one site, the burns killed all of the few oaks on the site, potentially greatly altering the habitat for wildlife using oak, despite the small statistical effect.

Data for logs in the pre-fire monitoring found that nearly 66 percent of all logs monitored were cut. These logs may have been the snags that were felled in the 1960s (general practice) to lessen wildfire threat from snags catching fire. They also may have been cull trees, which were felled during past logging. These logs were generally hard and full of pitch, which may have led to their loss. Many of these artificially-created logs might still be standing as snags or old-growth, if not for past fire prevention and cull policy.

Historical logging practices, especially the removal of large old-growth trees on many forested areas combined with fire prevention techniques, undoubtedly played a role in what we found. It is our opinion, based on the preliminary findings, that gains in logs and snags will only occur where there is abundant old-growth to allow for the conversions. It will take a long time to grow the trees to be old enough and large enough to get us out of this dilemma. Accumulated debris around the base of snags, oaks, and mature pines can greatly affect how hot the fires burn and how these habitat components are impacted (Harrington 1985, Horton and Mannan 1988). Dog hair thickets, stumps in the root zone, or thick duff areas may also be needed before enough heat is generated to cause the old-growth kill. Areas such as designated wilderness or stands with abundant old-growth trees will allow for gains in logs and snags.

Harrington and Sackett (1992) reported almost 40 percent old-growth ponderosa pine mortality at the Chimney Spring Prescribed Fire Research Area at Fort Valley. Their study took place within the same general area where we have been doing our monitoring. The duff layers and tree densities have been less in our study plots than in Harrington and Sackett's, study and one or both of these factors may account for any differences.

In Harrington and Sackett's (1992) study, mortality did not appear until several years after the burns; thus, a comparison with their results will be more appropriate after long term monitoring. To date, we have not found comparable heavy mortality in old ponderosa pine trees.

An unanswered question is how subsequent re-entries with prescribed fire will affect wildlife habitats. The most common thought is that fire events occurred in southwestern ponderosa pine every 7-15 years, and some managers would like to approximate that interval where possible. Our results raise a question about the gains and losses for logs, snags, oaks, and old-growth components with re-entry burns.

Management Implications

Through the evolution of our monitoring method, we have arrived at a relatively efficient means of monitoring the effects of prescribed fire on wildlife habitat. The use of a grid design, along with tagging each habitat component and sketch mapping each cell, proved much more efficient than the variable plot method for us. The grid with tagging and cell mapping may often be the best way for managers to obtain desired or required monitoring data on the effects of prescribed fire. The pre-burn setup time without the detailed data on each item should be about half what we currently need, and post-burn plot monitoring time should be cut by about 25 percent. We would estimate reducing the total time for setting up a plot and monitoring it twice to be approximately 8 person-days, or if the plot is read four times after the burn, 11 person-days. After the delay between the burn and expected tree mortality is worked out, two post-burn measurements may well be enough.

Forest managers should expect a decrease in logs and snags immediately after prescribed burning activities. Our data show that logs and snags will be reduced by approximately 50 and 20 percent, respectively. Managers should expect only a few logs or snags to be created immediately by the burn unless the site contains a high density of old trees and snags. Some additional snags and down logs may be gained later after the burn. Whether or not these changes in key wildlife habitat components are acceptable depends on how many are present before the fire.

The Stoneman burn, which experienced the lowest snag losses, had nearly every snag lined. Other Forest Service burns lined only some snags. It appears that lining may be an effective mitigation tool for reducing snag losses during prescribed burns.

Acknowledgments

Over the years, many field assistants from the Arizona Game and Fish Intern Program and Forest Service personnel have conducted field data collection. We appreciate all your excellent work. We especially thank Debbie Crisp who has helped to complete fieldwork every year and provided training to field crews. A special thanks to Chuck Benedict for assistance on the database housekeeping and the forest biologists on the Coconino for their continued support of this project. Numerous Forest Service personnel from the Kaibab and Coconino National Forests assisted with site selection and got these areas burned; thanks to George Sheppard, Larry McCoy, Jerry Bradly, Bob Smith and Andy Parker for helping us along. Also, thanks to Tom Ferrel at Walnut Canyon National Monument. Thanks to Steve Rosenstock, Joe Ganey, and Sandy Nagiller for reviewing this paper.

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Selection of Fire-created Snags at Two Spatial Scales by Cavity-nesting Birds[1]

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Abstract

We examined the use of snag stands by seven species of cavity-nesting birds from 1994-1998. Selection of snags was studied in logged and unlogged burned forests at two spatial scales: microhabitat (local vegetation characteristics) and landscape (composition and patterning of surrounding vegetation types). We modeled nest occurrence at the landscape scale by using Landsat Thematic Mapper imagery. At both spatial scales, we observed a continuum in habitat use with the extremes represented by black-backed and Lewis's woodpeckers. A range of habitat conditions characteristic of black-backed and Lewis's woodpeckers would likely incorporate habitat features necessary for nest occurrence of other members in the cavity-nesting bird community.

Introduction

Forests affected by wildfire, and subsequent salvage logging, became increasingly prevalent in the early 1990s across much of the inland West. Many cavity-nesting birds are associated with burned forests, but little is known about their habitat selection in post-fire conditions (Hutto 1995, Kotliar and others [In press], Saab and Dudley 1998). Virtually nothing is known about the influence of landscape patterns on nest-site selection in burned forests (Kotliar and others [In press]).

Species of cavity-nesting birds respond variably to post-fire salvage logging (Caton 1996, Hitchcox 1998, Kreisel and Stein 1999, Saab and Dudley 1998). Cavity nesters, however, often nest (Saab and Dudley 1998) and forage (Kreisel and Stein 1999) in patches of higher snag densities than that expected based on availability of snags. In salvaged forests of western Idaho, snags generally were retained in uniform distributions (equal numbers of snags per hectare), while within those burned forests,

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we previously reported that cavity-nesting birds used clumps (stands) of snags for their nest sites (Saab and Dudley 1998). We suggested that salvage prescriptions could be improved to favor cavity-nesting birds by changing the distribution of snags retained (from uniform to clumped), even when the same number of snags are harvested.

In this paper, we examine the use of snags by cavity-nesting birds at both the microhabitat and landscape scales within burned forests. A landscape-level analysis is necessary to estimate the area (size) and distribution of snag stands selected by cavity nesters. A large-scale analysis, however, is difficult in burned forests because snag stands are not easily detected with remote sensing. We have three related questions that address the area and distribution of snag stands. First, is pre-fire vegetation classification a reasonable index to post-fire stands of snags at the microhabitat scale? Second, using pre-fire vegetation classification, what are the characteristics of snag stands surrounding nest sites at the landscape scale? Lastly, are patterns of nest-site selection at the landscape scale consistent with patterns at the microhabitat scale? Information developed from this study is intended to provide guidelines for post-fire, snag management that accommodates cavity-nesting birds at two habitat scales: microhabitat (nest site) and landscape (composition and patterning of surrounding vegetation cover types).

Study Area

The study areas are in the Foothills and Star Gulch fires on the Boise National Forest in southwestern Idaho (Elmore, Ada, and Boise Counties). Elevation ranges from 1,100 meters to 2,400 meters. The Foothills fire was a moderate to high-intensity crown fire during August/September 1992 that burned 104,328 hectares. Prior to the fire, about a third of the burn was forested and the remainder was shrub steppe. The Star Gulch Fire occurred in August 1994 and burned 12,350 hectares at various intensities, creating a patchy mosaic of green and burned forest. Because of the nature of these fires, most standing trees were snags.

Pre-fire overstory vegetation was dominated by ponderosa pine *(Pinus ponderosa)* community types at lower elevations and on southerly aspects, whereas Douglas-fir *(Pseudotsuga menziesii)* community types dominated at higher elevations and on northerly aspects.

We selected at least two replicates each in unlogged and logged treatments. Seven study sites averaged 680 hectares in size, based on the area treated, and were used to monitor cavity-nesting birds and vegetation in post-fire conditions. One unlogged and four logged study sites were used in the Foothills study area, while two unlogged study sites were located in the Star Gulch study area.

Salvage logging prescriptions on the Foothills Fire varied by aspect and management for big game security cover (Saab and Dudley 1998). Based on the average densities of standing snags in unlogged units, about 50 percent of smaller snags (> 23 centimeters to ≤ 53 centimeters diameter breast height [dbh]) and 70 percent of larger snags (≥ 53 centimeters dbh) were harvested in the salvage-logged units (Saab and Dudley 1998). Densities of small snags averaged 43 per hectare and large snags averaged 5 per hectare in logged units, whereas densities in unlogged units averaged 81 per hectare for small snags and 17 per hectare for large snags.

Methods

Nest Monitoring and Microhabitat Measurements

Nest surveys for nine cavity-nesting birds *(table 1)* were conducted by walking 200 meter-wide belt transects during May through June 1994-1998. Transect length averaged 1.6 kilometers and number of transects per study site varied from 26 to 43. Nests were monitored every 3 to 4 days to determine status and fate. Methods for vegetation measurements and nest monitoring followed those described for BBIRD (Martin and Guepel 1993, Ralph and others 1993) with some modifications. The number and dbh of all snags > 23 centimeters were recorded within 11.3 meter-radius plots (0.04 hectare) centered at each nest tree. The same data were recorded at 89 non-nest random locations (40 in unlogged and 49 in logged treatments). Each nest tree and the center of each random location were geographically referenced by using a global positioning system (GPS), and data were exported into the geographic information system, ARC-INFO (Anonymous 1998).

Table 1—*Number of nests and non-nest random points monitored in burned ponderosa pine/Douglas-fir forests of western Idaho, 1994-1998.*

Species	Logged	Unlogged	Total
American Kestrel *(Falco sparverius)*	80	20	100
Lewis's Woodpecker *(Melanerpes lewis)*	305	50	355
Hairy Woodpecker *(Picoides villosus)*	46	135	181
White-headed WP *(Picoides albolarvatus)*	4	10	14
Black-backed WP *(Picoides arcticus)*	6	29	35
Northern Flicker *(Colaptes auratus)*	87	101	188
Western Bluebird *(Sialia mexicana)*	130	60	190
Mountain Bluebird *(Sialia currucoides)*	60	132	192
European Starling *(Sturnus vulgaris)*	31	0	31
Nest Total	749	537	1,286
Non-nest Random Points	49	40	89

Vegetation Classification and Landscape Measurements

Vegetation classification was derived from two Landsat Thematic Mapper (TM) images. Each TM pixel covers a 30-meter by 30-meter area. A pre-fire classification was mapped from a September 1991 image, and post-fire conditions were mapped from a September 1995 image. Aerial photography (1:16000) from July 1988 and August 1996 were used to assist in the classification process.

The vegetation classification had two components: (1) cover type, and (2) crown closure for each cover type. Decision rules for assigning cover types were derived from the Southwest and Central Idaho Ecogroups, who mapped 8 million hectares in southwestern Idaho (Redmond and others 1998). Cover types for our study included ponderosa pine, Douglas-fir, and a mix of ponderosa pine and Douglas-fir. The crown closure classes we used were: low (> 10 to ≤ 40 percent), moderate (> 40 to ≤ 70 percent), and high (> 70 percent). Ninety-eight training sites were visited in the field to calibrate the classified images.

Landscape measurements were determined from ARC-INFO files by using the landscape metrics software FRAGSTATS (McGarigal and Marks 1995). Landscape analyses were conducted only for black-backed and Lewis's woodpeckers because at the microhabitat scale, these species represented different ends of a continuum in habitat use (see Saab and Dudley 1998). Landscape variables were measured within a 1,000-meter radius of nest trees and random points, an area (314 hectares) that encompasses the home range sizes of most songbirds (Hansen and Urban 1992) and some woodpecker species in the Pacific Northwest of U.S. (Dixon and Saab 2000), Goggans and others 1989, Garrett and others 1996).

The resolution of TM imagery was too coarse for identifying stands of snags in the post-fire image. To describe stand area and distribution of snags and other landscape patterns, we developed a vegetation map by combining pre- and post-fire classifications. We used pre-fire cover type/crown closure as an index to post-fire composition and stand area of snags, based on nine cover type/crown closure classes: ponderosa pine/low, moderate, and high crown closure; Douglas-fir/low, moderate, and high crown closure; and ponderosa pine-Douglas-fir/low, moderate, and high crown closure. Based on earlier microhabitat findings (Saab and Dudley 1998), we wanted to know if high and moderate snag densities in burned forests at black-backed and Lewis's woodpecker nest sites, respectively, would correspond to high and moderate crown closure in pre-fire conditions.

For a measure of distribution of snag stands surrounding each nest and random point, we calculated the mean nearest neighbor and mean proximity index (McGarigal and Marks 1995) of like stands (same cover type/crown closure) for each of three cover types in moderate and high crown closures. Nearest neighbor was the mean distance (meters) to the nearest like stand, regardless of stand area, within the 1,000 meter-radius landscape circle. The mean proximity index considered the distance (meters) to and area (hectares) of like stands. This index measured both the degree of cover type isolation and the degree of fragmentation of the corresponding cover type within the 1,000 meter-radius landscape (McGarigal and Marks 1995).

Analyses

At the microhabitat scale, type III sums of squares, analysis of variance (ANOVA; Anonymous 1996) was used to test for non-random selection of snag densities by comparing densities at nest sites with random sites. Differences in habitat measurements for microhabitat and landscape variables were considered significant at $p < 0.05$. Means are followed by ± one standard error (SE).

For landscape analyses, we adopted the approach recommended by Burnham and Anderson (1998), i.e., we developed a "global" logistic regression model containing various landscape predictor variables that may have had important influences on nest occurrence of black-backed and Lewis's woodpeckers. Three global models were developed: nest occurrence of black-backed woodpecker vs. random points in unlogged units, nest occurrence of Lewis's woodpecker vs. random points in unlogged units, and nest occurrence of Lewis's woodpecker vs. random points in logged units. We were unable to model the response of black-backed woodpeckers to landscape features in logged units because of a small sample of nests (n = 6). Global models were tested for goodness of fit using the Hosmer and Lemeshow (1989) test. From the global model for each set of comparisons, we generated a subset of candidate models that contained various combinations of variables we deemed biologically relevant.

We used the Akaike's Information Criterion (AIC; Akaike 1973) to rank candidate models and assess their relative plausibility given the data. AIC operates on the principle of parsimony (Box and Jenkins 1970), where the highest ranked models are those that best fit the data with the fewest parameters. The principle of parsimony states that there is an ideal point in the balance between increasing the number of parameters to decrease bias and decreasing the number of parameters to increase precision. We used PROC LOGISTIC in SAS (Anonymous 1996) to produce AIC values for all sets of candidate models. Once we selected the best candidate model based on the highest AIC value, standardized estimates derived from logistic regression were used to evaluate the relative importance of each landscape predictor variable to nest occurrence (cf. Manly and others 1993).

Results

Microhabitat

To date, microhabitat data have been analyzed for 1994-1996 (625 nests, 89 random sites). Based on these data, seven species selected nest sites with significantly higher snag densities than that measured at random sites in both logged (d.f. = 7, F = 7.2, $p < 0.001$) and unlogged (d.f. = 7, F = 4.6, $p <0.001$) treatments *(fig. 1).* Snag densities were highest at black-backed woodpecker nest sites and lowest at random sites. Among cavity nesters, snag densities were lowest at Lewis's woodpecker nest sites, yet densities were still higher than those in the random unlogged controls. This suggests that cavity nesters as a group selected clumps (stands) of snags rather than uniformly-spaced snags (Saab and Dudley 1998).

Based on 1994-1995 data, we reported that cavity-nesting birds used larger diameter snags more than in proportion to availability (Saab and Dudley 1998). Among the woodpecker species, Lewis's woodpecker selected the largest diameter snags, whereas black-backed woodpecker used the smallest diameter snags. This pattern has continued through 1998: snag diameters were smallest for black-backed woodpecker and largest for Lewis's woodpecker *(fig. 2).*

Landscape

All global models adequately fitted the data (Hosmer and Lemeshow goodness of fit test, $p > 0.5$). The selected model for black-backed woodpecker in unlogged units included 15 predictor variables *(table 2).* Statistically significant predictors were proximity of stands characterized by burned, ponderosa pine/high crown closure; proximity; and area of burned, Douglas-fir/high crown closure stands; and area of burned, Douglas-fir/low crown closure stands. Standardized estimates derived from logistic regression indicate the strength and nature of the relationship between the predictor variables and the response variable. The strongest positive standardized estimates indicated that area and proximity of burned, Douglas-fir/high crown closure stands were the best predictors of black-backed nest sites in unlogged landscapes, whereas one would be unlikely to find a nest in close proximity of burned ponderosa pine/high crown closure or in stands of Douglas-fir/low crown closure *(table 2).*

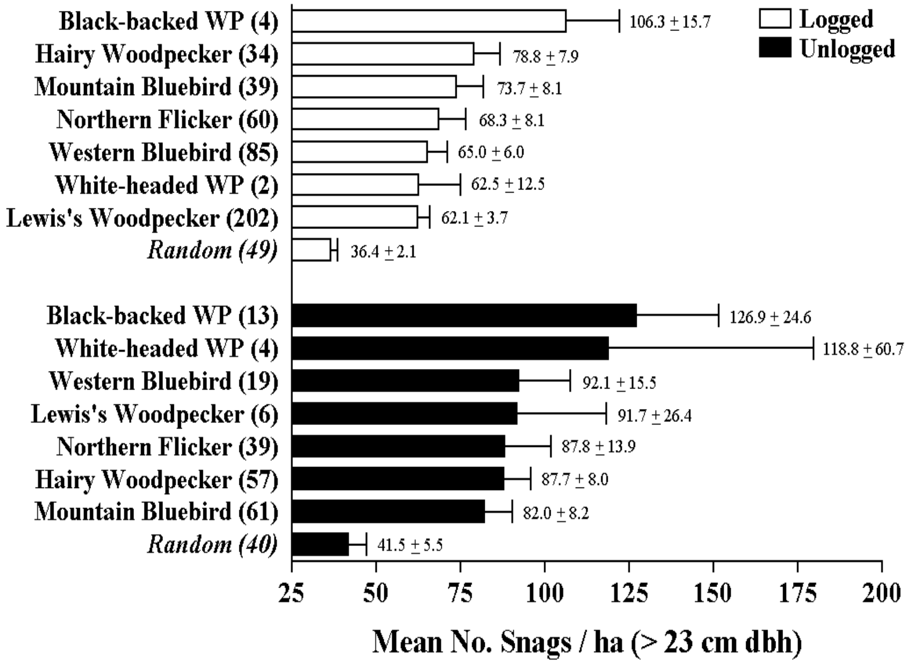

Figure 1—Mean number of snags (> 23 cm dbh) per hectare (+ 1 SE) surrounding nest trees and random trees based on microhabitat measurements during 1994-1996. Sample size for each species is stated in parentheses.

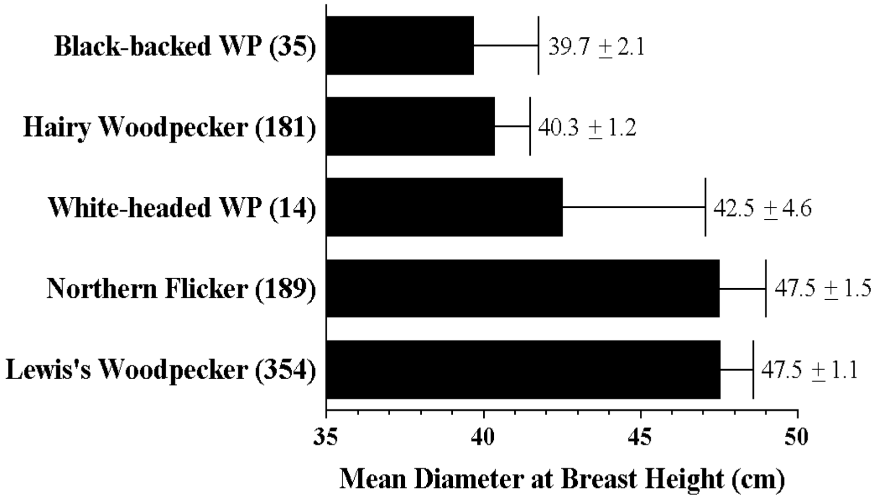

Figure 2—Mean diameter (± 1 SE) at breast height of nest trees during 1994-1998. Sample size for each species is stated in parentheses.

Table 2—*Selected models and coefficients derived from logistic regression for predictors of nest occurrence for black-backed woodpecker (unlogged) and Lewis's woodpecker (unlogged and logged).*

Variable	Parameter estimate	SE	Chi-square	P	Standardized estimate
Unlogged					
Black-backed Woodpecker (n=29 nests) vs. Random (n=40 points)					
Intercept	3.44	4.46	0.60	0.440	
Proximity Index-Ponderosa Pine High CC[2]	**-2.14**	**0.79**	**7.27**	**0.007**	**-2.55**
Proximity Index-Ponderosa Pine Moderate CC	0.02	0.10	0.05	0.820	0.13
Proximity Index-Doug-Fir High CC	**0.34**	**0.13**	**6.60**	**0.010**	**2.27**
Proximity Index-Doug-Fir Mod CC	0.27	0.69	0.16	0.690	0.22
Proximity Index-Ponderosa/Doug-Fir High CC	-3.33	1.83	3.31	0.070	-1.46
Proximity Index-Ponderosa/Doug-Fir Moderate CC	-1.83	1.08	2.82	0.090	-1.09
Stand Area-Ponderosa Pine High CC	-0.49	0.29	2.97	0.080	-2.21
Stand Area-Ponderosa Pine Moderate CC	-0.16	0.17	0.80	0.370	-1.26
Stand Area-Ponderosa Pine Low CC	0.21	0.12	2.84	0.090	1.64
Stand Area-Doug-Fir High CC	**0.47**	**0.21**	**4.90**	**0.030**	**4.64**
Stand Area-Doug-Fir Moderate CC	0.61	0.34	3.04	0.080	1.36
Stand Area-Doug-Fir Low CC	**-1.09**	**0.49**	**5.03**	**0.030**	**-11.7**
Stand Area-Ponderosa Pine/Doug-Fir High CC	0.56	0.59	0.87	0.350	0.84
Stand Area-Ponderosa Pine/Doug-fir Low CC	-0.03	0.17	0.03	0.860	-0.18
Distance to High or Moderate CC	-0.02	0.02	0.54	0.460	-0.24

Variable	Parameter estimate	SE	Chi-square	P	Standardized estimate
Unlogged					
Lewis's Woodpecker (n=50 nests) vs. Random (n=40 points)					
Intercept	6.63	7.00	0.90	0.340	
Nearest Neighbor-Ponderosa Pine Moderate CC	-0.13	0.08	2.38	0.120	-0.83
Nearest Neighbor-Doug-Fir Moderate CC	-0.01	0.07	0.03	0.860	-0.05
Nearest Neighbor-Ponderosa/Doug-Fir Moderate CC	0.001	0.05	0.00	0.990	0.009
Proximity Index-Ponderosa Pine Moderate CC	**0.12**	**0.06**	**4.03**	**0.040**	**0.77**
Proximity Index-Doug-Fir Moderate CC	0.4	0.49	0.66	0.420	0.31
Proximity Index-Ponderosa/Doug-Fir Moderate CC	-0.1	0.57	0.03	0.870	-0.05
Stand Area-Ponderosa Pine Moderate CC	**-0.22**	**0.11**	**3.83**	**0.050**	**-1.74**
Stand Area-Ponderosa Pine Low CC	0.13	0.09	2.05	0.150	0.87
Stand Area-Doug-Fir Moderate CC	-0.06	0.18	0.09	0.760	-0.11
Stand Area-Doug-Fir Low CC	-0.11	0.09	1.43	0.230	-1.08
Stand Area-Ponderosa Pine/Doug-fir Mod CC	0.14	0.22	0.45	0.500	0.49
Stand Area-Ponderosa Pine/Doug-fir Low CC	-0.03	0.08	0.11	0.740	-0.17
Distance to High or Moderate CC	-0.03	0.02	3.38	0.070	-0.43

(*table 2* continued)

Variable	Parameter estimate	SE	Chi-square	P	Standardized estimate
Logged					
Lewis's Woodpecker (n=305 nests)					
vs. Random (n=49 points)					
Intercept	3.26	1.40	5.36	0.020	
Nearest Neighbor-Ponderosa Pine High CC	**-0.03**	**0.01**	**7.50**	**0.006**	**-0.27**
Nearest Neighbor-Ponderosa Pine/Doug-Fir High CC	-0.003	0.00	1.60	0.200	-0.16
Stand Area-Ponderosa Pine High CC	**0.12**	**0.06**	**3.71**	**0.050**	**0.51**
Stand Area-Ponderosa Pine Moderate CC	0.04	0.05	0.48	0.490	0.22
Stand Area-Ponderosa Pine Low CC	-0.02	0.02	1.19	0.280	-0.24
Stand Area-Doug-Fir High CC	-0.02	0.02	0.78	0.390	-0.19
Stand Area-Doug-Fir Moderate CC	-0.04	0.07	0.27	0.600	-0.11
Stand Area-Doug-Fir Low CC	0.02	0.03	0.26	0.600	0.07
Stand Area-Ponderosa Pine/Doug-Fir High CC	**-0.37**	**0.09**	**16.04**	**0.001**	**-0.66**
Stand Area-Ponderosa Pine/Doug-fir Mod CC	**0.39**	**0.15**	**6.90**	**0.009**	**1.2**
Stand Area-Ponderosa Pine/Doug-fir Low CC	-0.09	0.06	2.27	0.130	-0.45

[1] The highest standardized estimates are in bold, indicating the most important predictors of nest occurrence.

[2] CC = Crown closure. Cover types were in burned conditions. Variables represent mean values.

One goal of the multivariate analysis is to statistically adjust the estimated effects of each predictor variable in the model for differences in the distributions of and associations among the other predictor variables (Hosmer and Lemeshow 1989). When adjusting for other variables in the model, stand area of burned, Douglas-fir/high crown closure was the most important variable in predicting the presence of black-backed woodpecker nests *(table 2).* Probability of nest occurrence was most consistently high for black-backed woodpecker when stand area of Douglas-fir/high crown closure was between 30 and 50 hectares *(fig. 3).* In landscapes where stand area was outside of this range, other landscape features necessary for nesting black-backed woodpeckers were likely reduced in availability or absent. Nests were not present where stand area was less than 12 hectares, and probability was highly variable when stand area was between 12 and 25 hectares or when area was greater than 55 hectares *(fig. 3).* The average stand area within landscapes surrounding black-backed nests was 37.16 hectares ± 3.41, whereas average stand area at random points was 24.87 hectares ± 3.7 *(fig. 4).* The stand area for all species of cavity nesters was between the areas measured for black-backed and Lewis’s woodpeckers *(fig. 4),* a pattern similar to that reported at the microhabitat scale *(figs. 1, 2).*

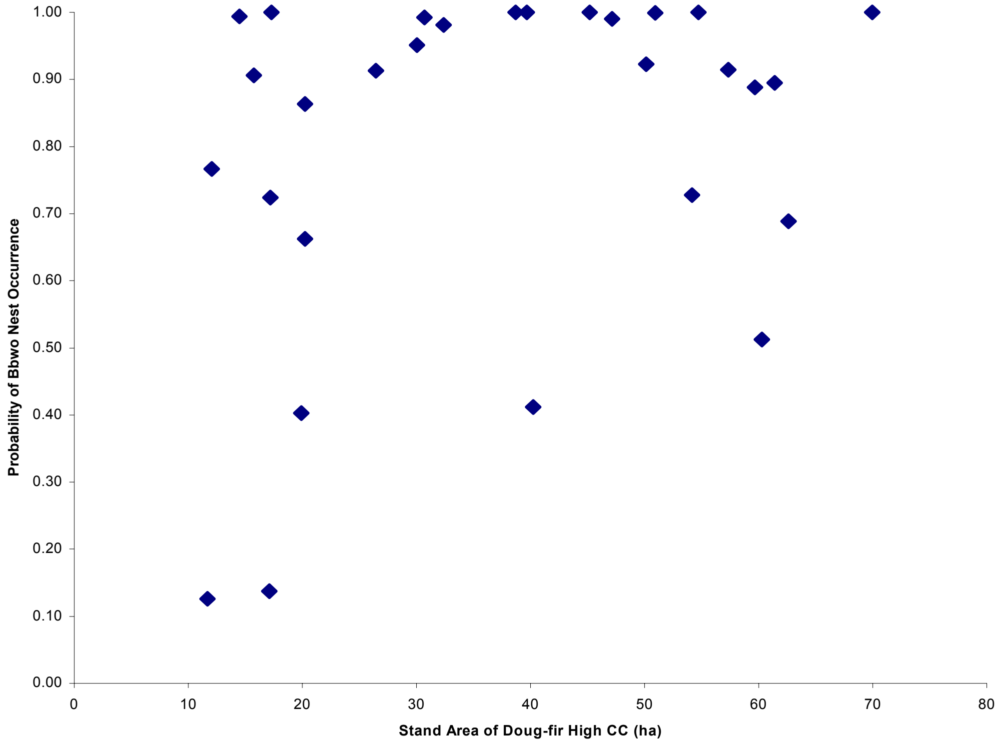

Figure 3—Scatter plot of the probability of black-backed woodpecker nest occurrence with stand area of burned, Douglas-fir/high crown closure areas. The scatter plot was adjusted for other landscape variables in the predictive model.

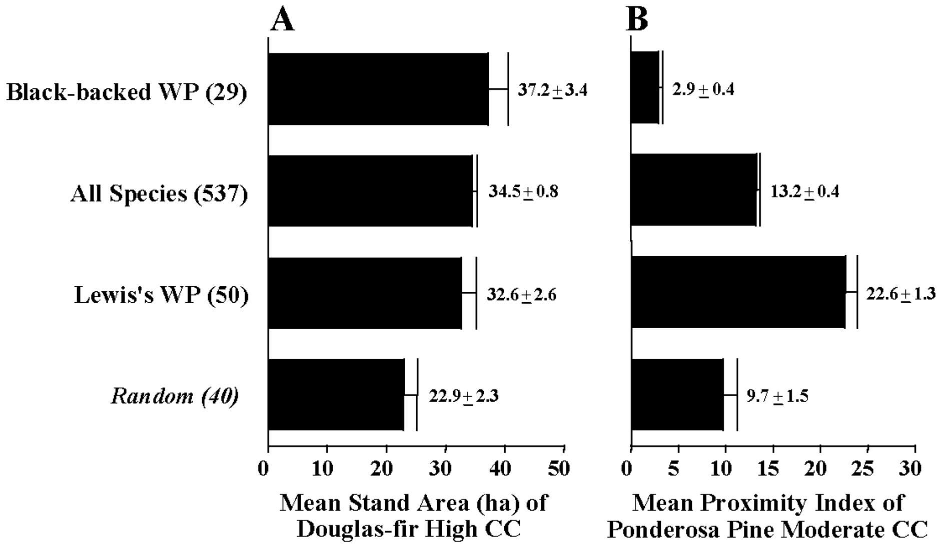

Figure 4—Based on measurements taken within landscape circles (1,000 meter-radius circle) surrounding nest and random points. (A) Mean area of stands (± 1 SE) characterized as burned, Douglas-fir/high crown closure, and (B) Mean proximity index (± 1 SE) of burned, ponderosa pine/moderate crown closure. Sample size for each species is stated in parentheses.

The selected model for Lewis's woodpecker in unlogged units included 13 landscape predictor variables *(table 2).* The only statistically significant predictor of their nest occurrence was the proximity of burned stands characterized by ponderosa pine moderate crown closure, while area of these stands was nearly significant at $p = 0.05$. Standardized estimates revealed that the strongest relationship between Lewis's woodpecker and the predictor variables was a negative one with area of burned, ponderosa pine/moderate crown closure stands *(table 2).* The mean area of these stands was 33.56 hectares ± 1.53 within nest landscapes, and 25.41 hectares ± 2.67 within random landscapes. The positive relationship with proximity of this cover type suggests that burned, ponderosa pine/moderate crown closure stands were in close proximity of one another within landscapes surrounding Lewis's woodpecker nests *(fig. 4).* This variable was not important to black-backed woodpeckers or all species combined. Once again, measurements revealed a similar pattern as that reported at the microhabitat scale: Lewis's woodpecker was at one end of the continuum of habitat use and black-backed woodpecker at the other end *(fig. 4).*

Eleven landscape predictor variables were included in the selected model for Lewis's woodpecker within logged units *(table 2).* Statistically significant predictors and the nature of the relationship with Lewis's woodpecker were:

- Nearest neighbor of burned, ponderosa pine high crown closure stands, negative relationship.
- Area of burned, ponderosa pine high crown closure stands, positive relationship.
- Area of burned, ponderosa pine/Douglas-fir high crown closure, negative relationship.
- Area of burned, ponderosa pine/Douglas-fir moderate crown closure, positive relationship.

Based on standardized estimates, area of ponderosa/Douglas-fir moderate crown closure stands (mean = 6.63 hectares ± 0.16) was the most important variable in predicting nest occurrence of Lewis's woodpecker in logged units. Thus, regardless of cover type or treatment, moderate crown closure in a burned condition was the most important characteristic of a landscape feature in predicting the presence of a Lewis's woodpecker nest. The negative relationship with nearest neighbor of burned, ponderosa pine/high crown closure and the positive relationship with stand area of the same cover type/crown closure indicates that the close distribution (mean nearest neighbor = 61.9 meters ± 0.75) and large area (mean = 15.82 hectares ± 0.47) of these stands was also important for their nest site selection.

Discussion

At the microhabitat scale, habitat use by black-backed and Lewis's woodpeckers was represented by different ends of a continuum. Compared to other cavity-nesting birds and random sites, black-backed woodpeckers selected nest sites with the highest densities of snags of relatively small diameters, whereas Lewis's selected nest sites with moderate densities of snags of large diameters. The microhabitat selection by black-backed woodpeckers that we observed in western Idaho is similar to that reported elsewhere in the Northern Rocky Mountains. Black-backed woodpeckers have consistently selected unlogged conditions of high snag densities for both nesting and foraging habitat (Caton 1996, Hitchcox 1996, Hoffman 1997, Hutto 1995, Kreisel and Stein 1999). Perhaps high snag densities provide greater foraging opportunities for this species (Saab and Dudley 1998) that feeds primarily on bark (Scolytidae) and wood-boring (Cerambycidae) beetles (Dixon and Saab 2000). In contrast, Lewis's woodpecker favors open woodlands, especially burned pine forests (Tobalske 1997, Saab and Vierling 2001). Unlike most woodpecker species, Lewis's woodpeckers are primarily aerial flycatchers during the breeding season. This species is thought to do well in burned forests because of the relatively open canopy that allows for shrub development and associated arthropod prey (Bock 1970), good visibility, and perch sites for foraging (Linder and Anderson 1998), and space for foraging maneuvers (Saab and Dudley 1998).

Pre-fire crown closure of live trees may serve as an index to post-fire stand densities of snags. One might expect that unburned stands of Douglas-fir with a high crown closure could result in burned high densities of snags with relatively small diameters. This was consistent with black-backed woodpecker nest-site selection at both the microhabitat and landscape scales in burned forests of western Idaho. Likewise, one might expect that unburned moderate crown closure stands of ponderosa pine and Douglas-fir could result in burned moderately dense stands of snags with relatively large diameters. This characterized nest-site selection by Lewis's woodpecker at the microhabitat and landscape scales. Patterns in nest-site selection at the landscape scale were consistent with patterns in nest-site selection at the microhabitat scale. Following the microhabitat data, landscapes used by nesting black-backed woodpeckers represented one end of a habitat continuum, while landscapes used by Lewis's woodpeckers represented the other extreme.

Because pre-fire vegetation classification was a reasonable approximation of post-fire stands of snags, we used Landsat TM images of pre- and post-fire conditions to characterize the area and spatial distribution of snags surrounding nest sites. In unlogged burned conditions, black-backed woodpeckers selected landscapes where large stands of Douglas-fir/high crown closure occurred in closer proximity than in landscapes surrounding random points. Lewis's woodpeckers chose burned landscapes where relatively small stands of ponderosa pine/moderate crown closure were in close proximity compared to average, unlogged conditions.

In logged areas, moderate crown closure was again an important feature of landscapes surrounding Lewis's woodpecker nests. Stand area, however, was smaller on average in logged compared to unlogged units. The close distribution and large stand area of ponderosa pine/high crown closure was another important characteristic of landscapes surrounding nests of Lewis's woodpecker in logged conditions. Stands of burned, ponderosa pine/Douglas-fir with moderate crown closure were the best predictor of Lewis's woodpecker nests.

Management Implications

The continuum of habitat use by black-backed and Lewis's woodpeckers reported for the microhabitat scale was consistent at the landscape scale. This suggests that management for cavity nesters should be considered not only at the local, stand level but also at larger spatial scales. At both scales, we found that a range of habitat conditions characteristic of black-backed and Lewis's woodpeckers would likely incorporate habitat features necessary for nest occurrence of other members in the cavity-nesting bird community.

Our data suggest that pre-fire vegetation classification can be used to develop design criteria for cavity-nesting birds in post-fire salvage logging projects. We can manage for a diversity of species across burned landscapes by maintaining a continuum of habitat features. Unlogged landscapes with large, dense stands of Douglas-fir snags in close proximity to one another were typical of black-backed woodpeckers. Partially logged landscapes were favored by Lewis's woodpeckers, although they selected unlogged conditions for nesting habitat as well. Burned landscapes used by nesting Lewis's woodpeckers were primarily composed of closely distributed, small to medium-sized stands of ponderosa pine/moderate crown closure.

Our future work will be focused on examining the relationships between pre-fire crown closure (from remote sensing) and post-fire snag densities and diameters (from our microhabitat measurements). Determining these relationships will assist not only in developing design criteria for post-fire salvage logging but also in generating stand exam information based on remote sensing data. Future work also will include developing probabilities of nest occurrence for each species using landscape variables and examining the influence of landscape variables on nest success.

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Dead Tree Management in British Columbia[1]

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Abstract

We highlight the historical development, current legislation, and operational practices regarding dead tree management in British Columbia (BC), Canada. BC's Forest Practices Code, which regulates forest management, enables resource managers to leave wildlife tree patches in harvested areas, and to consider the retention of coarse woody debris (CWD). At the same time, occupational health and safety regulations govern the retention of potentially dangerous trees in forestry operations, and current CWD policy enables the management of CWD only within harvesting utilization standards. Managing for the ecological values of dead trees without impacting timber supply is a challenge facing BC's forest managers.

Introduction

British Columbia (BC) is Canada's most ecologically and biologically diverse province, with areas of extensive alpine, rangeland, and forest. Ownership of the province's 95.2 million ha is predominantly public (94.7 percent). These lands are administered for many purposes including fish, wildlife, wilderness, recreation, heritage, water, minerals, range, and timber. The Ministry of Forests (MOF) manages, in cooperation with other provincial and Federal agencies, the timber, range, and recreation resources of the unreserved public forest land (about 59 million ha). From these lands about 65-70 million cubic meters of wood are harvested annually (Ministry of Forests 1998). The predominant (about 90 percent by area) silvicultural system is clearcutting or clearcutting with reserves of individual or clumps of trees.

The ecological values of dead trees are well recognized by the managers of BC's forests. Wildlife trees (standing dead trees and live defective trees) are a vital component of biodiversity, providing critical habitat for 80 species of birds,

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mammals and amphibians in BC, as well as habitat for a myriad of invertebrate and fungal organisms (Lofroth 1998, Machmer and Steeger 1995). Coarse woody debris (CWD; fallen dead trees) has similar critical roles for many species of plants (especially bryophytes and lichens), fungi, invertebrates, and small mammals (Harmon and others 1986, Stevens 1997). The value of dead wood, particularly for wildlife trees, is acknowledged in forest management in BC through regulations issued under legislative acts.

In this paper, we outline the history and status as of December 1999 of the legislation and management of dead wood on crown lands in BC.

History of Forest Management and the Dead Wood Resource

Forests provided important resources to the First Nations of BC in terms of housing, transportation, clothing, household goods, fuel, and food. Dead wood was valued for a variety of purposes. Turner (1998) identified specific uses of dead wood that include cottonwood *(Populus balsamifera* ssp. *trichocarpa)* for the hearth and drill for creating friction fires, rotten trembling aspen *(P. tremuloides)* as an absorbent material, decayed wood for smudge for tanning hides, and knots left in rotten western hemlock *(Tsuga heterophylla)* and spruce (*Picea* spp.) logs for curved fish hooks. Little has been summarized specifically on the management of dead wood by First Nations, whose population was likely between 200,000 and 300,000 in the mid-1700s (Muckle 1998). Undoubtedly forest management did occur, given the recognition of resource ownership by many First Nations. Prescribed burning was carried out for a number of purposes—primarily to create and/or maintain certain vegetative types and to clear the land around habitations. Single burns would add to the dead wood resource, while repeated burning would reduce levels of both standing and downed material.

Commercial forest harvesting in BC began in earnest in the late 1800s. It was concentrated in the valuable and easily-accessible timber of the west coast and at lower elevations of major valleys in the interior of BC. Impacts on the forest were generally low because only the more valuable and easily-transported trees were cut. Undesirable species may have been felled to provide a cushion and reduce breakage of valuable trees felled subsequently. A legacy of high stumps was left due to the use of springboards to cut above butt flares. Additionally, the lower portions of felled trees were sometimes too massive to move and so were left in place. This increased the proportion of large diameter, fresh CWD in forests.

The use of high-lead yarding and extensive railway logging networks began just before World War I, ushering in clearcutting as a harvesting system. At the same time, slashburning was promoted by the BC Forest Service to reduce the fire hazard on logged coastal sites. The application of fire was deemed appropriate to remove fuels and create a seedbed amenable to natural regeneration. Some CWD would be removed by these controlled burns, but given that partial cutting (essentially high-grading) was still common, a supply of fire-killed standing dead trees was created at the same time.

Fire prevention has been encouraged since 1905, when fire wardens were first appointed. Early controlled burning reduced logging slash loadings but escaped burns increased dead wood resources. Human-caused wildfires have done likewise. Effective fire suppression began in the late 1950s due to improved fire detection, technological advancements, such as air tankers and lightweight fire pumps. While the number of wildfires has increased since the late 1950s (from an average of 1,583 per year in the 1940s and 1950s to 2,493 in the 1980s and 1990s), the area burned has dramatically declined. Total area burned for the respective periods was 3,000,462 ha and 1,265,573 ha, as average fire size decreased from 94 to 25 ha.

Artificial reforestation was initiated in coastal BC in 1939 and in the Interior in 1950. To reduce the fire hazard and improve safety for planting crews, snags were felled on parts of Vancouver Island as early as 1942. In 1946 the Forest Act was amended to make snag falling compulsory concurrent with logging operations in the Vancouver Forest District (Statutes of British Columbia 1946). All standing dead trees taller than 10 feet were felled, that being the height to which a man could apply dirt with a shovel to extinguish a burning snag.

By 1947, changing logging methods, closer utilization and salvage operations had reduced the amount of logging residue. A 1943 pulpwood salvage study found that salvable wood accounted for 19 percent of the total utilizable stand volume, the rest having been taken in the first pass for sawlog production (MacBean 1946). Slash burning became less common on the Coast and was replaced either by spot burning or no burning at all. This increased the amount of remaining medium-sized CWD. Snag falling continued, largely as a fire prevention and safety measure, resulting in most dead wood being on the ground and little left standing.

Environmental concerns became more prominent in the mid-1960s and early 1970s. Resource management guidelines dealt primarily with wildlife habitat, soil conservation, stream protection, riparian zone management, silvicultural systems, cutblock size and arrangement and road location. The general guidelines did not address site-specific issues such as CWD or wildlife trees, which had not yet been identified as items requiring consideration and management. Indeed, in 1978 the responsibility to "fall snags progressively with the felling of adjacent live timber" in all forest operations was entrenched in the Workers' Compensation Board (WCB) Industrial Health and Safety Regulations (Workers' Compensation Board of British Columbia 1998).

The Ministry of Forests Act of January 1, 1979 instructed the Ministry of Forests to integrate and coordinate the management of timber, range, fisheries, wildlife, water, outdoor recreation and other natural resource values (Revised Statutes of British Columbia 1979). Integrated use involved altering harvesting prescriptions to provide benefits to established resource users, mitigating the effects of harvesting, and facilitating change in forest conditions to support new uses. The main variables were dispersal of activities, size of cutblocks, time interval between the sequential removal of adjacent blocks and location of roads and other infrastructure (Ministry of Forests 1984). All of these are landscape level issues and no provisions specifically addressed the conservation of dead trees.

General recognition of the ecological importance of dead trees started to emerge in BC in 1979, following the lead of research and management in the U.S. Pacific Northwest. In February 1979, Kamloops Forest Ranger Jack Weinard initiated a process he called the "rule of thumb" for snag management in the Kamloops Ranger District (Stevenson 1999). In the 1980s, the Ministry of Forests and Ministry of Environment jointly developed a wildlife tree signing program. This involved placement of "Wildlife Tree: Do Not Disturb" signs on selected wildlife trees (Backhouse and Lousier 1991). In 1985 the BC Wildlife Tree Committee, a multi-agency group, was formed to consider the conservation and management of wildlife trees—particularly as related to their safe maintenance within forest operations (Manning 1995). This committee was instrumental in raising awareness of the need for legislation, regulations, guidelines and the importance of management of the dead tree resource.

In the 1990s the importance of dead trees was recognized through significant policy, management, and legislative change. A problem analysis by Backhouse and Lousier (1991) highlighted the importance of wildlife trees and the need for changes in wildlife tree management. The initiatives of the multi-agency BC Wildlife Tree Committee began to take root. Through interpretation of the term “hazardous,” the WCB began to recognize that not all standing dead trees were dangerous and that standing dead trees had ecological value. Wildlife/danger tree assessment procedures and training programs were initiated (Manning 2002). Management for wildlife trees began to appear in regional and provincial guidelines.

Initiatives for CWD have lagged behind those of wildlife trees in BC. In fact, the Ministry of Forests initiated and still has in place a strict residue and waste policy as part of its utilization standards (Caza 1993). This policy requires licensees to remove all wood above certain size and soundness limits while harvesting and penalizes them if they do not.

Current Legislation and Regulations

In 1995, BC introduced major changes to the legislation affecting forest resource management with the implementation of the Forest Practices Code of British Columbia Act. The Forest Practices Code establishes mandatory requirements for planning and forest practices, sets enforcement and penalty provisions, and specifies administrative arrangements. The regulations under the act lay out the forest practices that apply province-wide, including the planning framework. This act applies to all crown lands outside of protected areas, or about 80 percent of the land base in BC (Fenger 1995).

Guidance for planning is provided in a number of ways, including forest practices guidebooks and various levels of policy. This guidance is not normally binding until it is written into a higher level plan or operational plan (see http://www.for.gov.bc.ca/tasb/legsregs/fpc/hilevel/hlp-toc.htm for a detailed outline of the hierarchy under the Forest Practices Code). Landscape Unit Planning is the higher level process that sets the legal requirements for wildlife tree retention and old-growth management. Landscape Units usually cover a watershed or a series of watersheds and average about 70,000 ha. Other higher level plans (e.g., Local Resource Management Plans that address a region with many landscape units) may also provide direction on dead tree management. Further guidance for wildlife trees and CWD is found in Forest Practices Code documents, such as the *Biodiversity Guidebook*, *Riparian Management Area Guidebook*, and the *Identified Wildlife Management Strategy* (Ministry of Forests and BC Environment 1995a, 1995b, 1999).

The importance of wildlife trees is well recognized within Forest Practices Code regulations and guidelines. The Forest Practices Code of British Columbia Act and associated regulations provide the framework for wildlife tree management by ensuring that wildlife tree objectives are stated, that wildlife tree and other reserves are clearly mapped within operational plans and marked in the field, and that penalties for non-compliance are in place *(table 1)*. Further, changes made in April 1998 to the WCB Occupational Health and Safety Regulations now enable greater retention of standing dead trees that do not pose a safety hazard *(table 2)*.

Table 1—*Forest Practices Code of British Columbia Act and associated regulations that relate to dead trees (the act and regulations are available at http://www.for.gov.bc.ca/tasb/legsregs/comptoc.htm).*

Act or Regulation	What
Forest Practices Code of British Columbia Act	12. A silviculture prescription must comply with the following: (a) it must include, for the area under the prescription, (i) long term management objectives set out (A) in a Forest Development Plan… (ii) a description of the silvicultural system and post harvesting stand structure and site condition 41(1)(b) "the district manager is satisfied that the plan or amendment will adequately manage and conserve the forest resources of the area to which it applies." 41(2) before approving a plan or amendment the district manager may require the holder to submit information that the district manager reasonably requires in order to determine if the plan or amendment meets the requirements of subsection (1)
Operational Planning Regulation	Section 1 - Definitions: "wildlife tree" means a tree or group of trees that are identified in an operational plan to provide present or future wildlife habitat 18(1) A person must ensure that a forest development plan includes the following information for the area under the plan: … (u) the general objectives respecting the target levels of retention for coarse woody debris and wildlife trees 32. A person must ensure that a logging plan contains a map of the area under the plan illustrating the topography and … (b) the approximate location of (i) mappable reserves including wildlife trees and wildlife tree patches 39(2) A person must ensure, for the area under the silviculture prescription, that the silviculture prescription describes the location of the following: … (d) mappable reserves, including wildlife tree patches and riparian reserve zones 39(3) A person must ensure, for the area under the silvicultural system, that the prescription does the following … (c) describes the silvicultural system to be used, including the species and function of any trees left standing. … (m) describes (i) the volume and range of piece sizes of coarse woody debris, if any, necessary or required to accommodate any objectives for coarse woody debris established in a forest development plan and that are applicable to the area under the prescription 50(2) A stand management prescription must … (b) contain a map illustrating … (ii) for the area under and adjacent to the prescription, the following items: … (D) the approximate location of mappable reserve areas, including wildlife tree patches
Timber Harvesting Practices Regulation	3(1) A person carrying out harvesting must mark in the field, before commencement of harvesting, the location of all wildlife trees or wildlife tree patches that are (a) 0.25 hectares or more, unless exempted by the district manager, and (b) less that 0.25 hectares, if required by the district manager (2) A person required to mark a wildlife tree or wildlife tree patch, under subsection (1) must ensure that the marking is visible during harvesting and is marked in a manner that will remain visible for at least 6 months after the completion of harvesting 28. A person must not carry out a minor salvage operation in any of the following areas unless harvesting the area has been approved in a silviculture prescription or the person has received in writing from the district manager the terms and conditions that apply to the carrying out of the minor salvage operation: … (c) wildlife tree patches;
Timber Harvesting Practices Regulation (Administrative Remedies Regulations Schedule)	Harvesting or damaging trees that are required by the silviculture prescription to be left standing or undamaged—$5000. Failure to mark in the field the location of wildlife trees or wildlife tree patches, before commencement of harvesting operations—$5000

Table 2—*Workers' Compensation Board Occupational Health and Safety Regulation as related to dead trees (these regulations can be viewed at http://www.worksafebc.com/policy/regs/contents.asp).*

Act or Regulation	What
Workers' Compensation Board Occupational Health and Safety Regulation	26.11(1) If work in a forestry operation will expose a worker to a dangerous tree, the tree must be removed. (2) Trees that will interfere with rig-up, the movement of lines and equipment, or that could be pushed or pulled into the work area must be removed. (3) Saplings over 6 m (20 ft) tall, in an area where cable logging is being done, must be removed before yarding commences. (4) If it is not practicable to comply with subsection (3), such as during partial cutting operations, alternative work methods or procedures which minimize the risk to workers may be used, and the work must be directed by a supervisor who has, as far as practicable, controlled the danger to any worker. (5) Any dangerous tree, regardless of height, located within an active hand falling or cable logging operation must not interfere with safe falling or yarding practices, and if it does interfere, it must be removed. (6) A dangerous tree in a forestry operation may be left standing during operations other than construction or harvesting if (a) no significant ground vibrations are likely to be produced, (b) no work will be done within reach of the tree when wind speed exceeds 20 km/h (12mph), and (c) tree assessor who has completed a training program acceptable to the board determines that the tree will not be dangerous to workers during the planned activity (7) If tree planting is to be done in an area that has more than 500 dangerous trees per hectare, the board may approve a request to work without removing all the dangerous trees if, before work commences, (a) a representative sample of the dangerous trees is assessed by a tree assessor who has completed a training program acceptable to the board, (b) any findings of the assessment as to the removal of dangerous trees or other trees are implemented, and (c) no silviculture is done within reach of dangerous trees when wind speed exceeds 20km/h (12 mph).

The importance of CWD is also clearly recognized within the Forest Practices Code regulations but, unlike wildlife trees, detailed provincial CWD management guidelines are lacking. References to CWD management within the *Biodiversity Guidebook* and the *Managing Identified Wildlife Guidebook* are less specific than references to wildlife trees. Several interim CWD guidelines have been drafted, but consensus has not been reached (see http://www.for.gov.bc.ca/research/deadwood/Dtgui.htm#BC for the current short-term strategy). Concerns not only also exist where specific CWD volume retention targets may conflict with present timber utilization standards as expressed in Ministry of Forests policy, but volume retention targets also conflict with wood below the standards that the forest licensees consider economical to harvest (Ministry of Forests Policy 8.1—Timber utilization—coastal and interior available at http://for.gov.bc.ca/tasb/manuals/policy/resmngmt/rm8-1.htm).

Current Management

Wildlife tree management includes both the retention of suitable trees at the time of harvest and during silviculture activities, and provision for recruitment of suitable replacement wildlife trees over the harvest rotation period. Operationally, there are three types of wildlife tree management strategies. These are wildlife tree patches (WTPs), individual live tree retention, and artificially created wildlife trees. Potentially, all three approaches can be applied in a single harvest area, although WTPs are generally the most operationally feasible (i.e., easier to accommodate various block layouts, topographic considerations, and harvesting methods) and the safest method for forest workers to retain wildlife trees. If selected carefully, WTPs can incorporate all or some of the habitat attributes commonly associated with the conservation of biodiversity at the stand level. These attributes include horizontal and vertical stand structure, wildlife trees, CWD, intact forest floor, and various special habitats, such as riparian areas, wetlands, gullies and rock outcrops. However, given our understanding of the ecological values of wildlife trees, it is prudent to also retain dispersed single trees within the landscape.

In 1995 the Biodiversity Guidebook brought forward a tabular approach to determining wildlife tree retention requirements for a particular area. Two variables must be known to allow determination of wildlife tree retention:

- Percent of the area available for harvest (i.e., percent of the total area deemed to be operable).
- Percent of the operable area already harvested without wildlife tree retention.

Knowing these numbers, an area retention objective ranging from 1 percent (where most of the area is inoperable and very little harvesting without wildlife tree retention has occurred) to 15 percent (where the area is highly operable and a large portion has been harvested without wildlife tree retention) is determined. These retention objectives can be applied as area-based WTPs or as a basal area equivalency for individual tree retention.

To date, Ministry of Forests district managers have generally provided policy as per the retention objectives and communicated them to licensees for incorporation into their silviculture prescriptions (an operational plan required prior to harvesting). With the recent issuance of the Landscape Unit Planning Guide, these will now be incorporated as landscape unit objectives (Ministry of Forests and Ministry of Environment, Lands and Parks 1999).

A silviculture prescription map must show the location of the WTPs that make up the retention objective and state the basal area equivalence for single tree management. A significant proportion of this retention will come from inoperable areas, such as riparian reserves. In addition, placement of wildlife tree patches should consider:

- Worker safety; only wildlife trees which are assessed as safe may be left outside of a patch within the work area.
- Location of good wildlife tree attributes, e.g., center a patch around a well-used wildlife tree or group of wildlife trees.
- Areas of tree species that are potentially valuable as wildlife trees and relatively uncommon.

- Stability of chosen patch, e.g., it may be advisable to locate patches adjacent to standing timber of a riparian reserve if there is concern regarding windthrow.

The decision to retain individual trees as wildlife trees in a harvest block will depend on the characteristics and condition of those trees (e.g., species, size, evidence of wildlife use, branching structure, decay, wind firmness, and safety considerations), and other management objectives (e.g., type of silvicultural system, harvesting method, and rotation length). In most cases, individual trees must be retained through the rotation in order to receive credit as wildlife trees in the management prescription. However, except for initial layout and considerations for wind firmness, no long-term management prescriptions for wildlife tree patches have usually been expressed.

In BC, hazard/danger tree assessment procedures developed by the Wildlife Tree Committee of BC are in place, along with appropriate training, concerning the management and retention of wildlife trees (Manning 2002). These guidelines are intended to provide information and technical procedures for assessing and safely retaining trees (some of which are potentially dangerous) in all types of forestry operations.

In some circumstances, trees are artificially modified to create or enhance wildlife tree habitat values. Methods used in BC include tree-topping, fungal inoculation, girdling, "planting snags" with an excavator, or cutting stems at 3 to 6 metres in height ("stubbing") with a mechanical harvester (Deal 1995, Harris 1995). The practice of modifying trees is usually only undertaken to remove specific safety hazards, or to augment other methods of habitat retention.

CWD management is less advanced than wildlife tree management, particularly due to the lack of CWD management guidelines. However, CWD objectives must be defined in forest development plans that guide individual silviculture prescriptions. CWD objectives must be balanced with other potentially competing stand management objectives such as fuel management.

CWD objectives defined in forest development plans range from general statements to more specific CWD volume retention targets. CWD volume targets are usually based on a volume that can be easily achieved within standard operational practice or a minimum of the range found in unmanaged primary forests (Stevens 1997). At present, forest companies are encouraged to leave behind as much CWD as possible provided it does not exceed the minimum utilization standards or interfere with other stand management objectives (i.e., forest health). This may be perceived as the status quo and often leads to the development of vague CWD management objectives, although it does not necessarily translate into low CWD retention.

In the case of general CWD management objectives—such as "within the requirements of normal utilization standards the licensee will try to maintain current levels of CWD on each cutblock providing post-treatment objectives, forest health, and fire hazard are not compromised"—the result on the ground depends greatly on the type of stand harvested, the pulpwood market, the harvesting and site preparation techniques, and the knowledge of the operators. For example, the whole-tree harvest of a 60-year old lodgepole pine (*Pinus contorta* var. *latifolia*) stand that has a history of underburn fires and, similarly, the harvest of coastal second-growth stands which were subjected to shake salvage will often result in very low post-harvest levels of CWD. On the other hand, clear-cut harvesting of a high elevation subalpine fir *(Abies* *lasiocarpa)* stand with many standing dead trees will generally yield high levels of CWD.

Communication between on-the-ground operators, foresters, and ecologists is important to minimize the adverse impact on the CWD resource and to maximize timber use. However, such communication varies within BC. Through communication, the experience of the operators plays an important role in the retention of CWD. An experienced on-the-ground operator may be able to leave uneconomic wood at the stump rather than hauling it to the landing by identifying only economic grade logs that should be yarded to the roadside, bucking out unmerchantable sections on the site, and retaining full-length intact uneconomic logs (Arsenault 2002).

Regulations and guidelines not only direct on-the-ground decisions but are considered in higher level forest management decisions, such as the determination of the allowable annual cut (AAC). In British Columbia, the AAC is determined by the Chief Forester of BC every 5 years for each of the 70 forest management units administered by the Ministry of Forests. To assist the decision of the Chief Forester that is based on social, economic, and ecological considerations, a timber supply review is conducted. The timber supply review uses simulation models in which the timber flow (merchantable volume that excludes most endemic dead wood) of the unit is projected. The models use current forest cover inventory and constraint information that reflect existing management practices, such as cutblock adjacency and ungulate winter range requirements, to model current and future timber flows (although the AAC decision is only for the first 5-year period).

In the timber supply review, wildlife tree patch requirements are commonly modeled by reserving a percentage of forest within a biogeoclimatic subzone in a landscape unit. CWD has not been considered directly as operational practices do not directly influence the merchantable volumes attributable to the AAC. Current practice has only used uneconomic CWD below utilization levels, though recent relaxation of utilization accounting could enable the retention of small volumes of some lower grades of wood. Non-recoverable losses, such as those caused by pest or fire, are excluded from the timber flow projections.

Management Support

Forest management planning in BC is supported by a variety of inventories, surveys, and projection tools. In the 1990s, under the auspices of the multi-agency Resources Inventory Committee, BC initiated substantial standardization and updating of resource inventories. The new provincial Vegetation Resources Inventory, that is to replace an existing provincial forest cover inventory, includes provision for both wildlife tree and CWD sampling (Ministry of Forests 1999). However, the majority of ground-based samples are expected to have a timber emphasis and not include items such as CWD. Procedures for describing terrestrial ecosystems include wildlife tree and CWD sampling (Ministry of Forests and Ministry of Environment, Lands and Parks 1998). Pre-harvest timber cruises provide counts of standing dead trees but typically only those with >50 percent sound wood. Similarly, post-harvest residue and waste surveys only sample merchantable wood volumes. Standards for growth and yield permanent sample plots were modified in 1999 to include standing dead tree measures. This information will be used to enhance existing standing and down dead tree models incorporated in growth and yield models used in forest management planning (Stone and others 2002). Although there is an expectation of improved dead tree information, these new sampling procedures need to be evaluated to ensure their usefulness.

Research on dead trees and their ecological values is conducted by the many research organizations in BC: provincial and Federal governments, academia, industry, and consultants. Little research on CWD was conducted in BC prior to the 1990s (Candy and Swan 1995, Caza 1993), although as early as 1929 MOF researchers showed some interest in CWD dynamics (Stone and others 1998). The past decade has seen increased research on the roles and dynamics of dead trees in BC and limited investigation of the effects of current harvesting practices on dead wood volumes and attributes. Forest Renewal BC, a Crown corporation established in 1994 that derives monies from stumpage revenues, has funded a variety of recent research on dead wood, including experimental manipulation of CWD, snag dynamics, CWD dynamics, the ecology of dead wood dependent organisms, and forest productivity relationships (Feller 1977, Huggard 1999). However, we still lack knowledge of the specifics of many of the ecological roles and dynamics of dead trees in conjunction with forest stand development and management (Lofroth 1998).

Education about dead trees has occurred at many levels in BC. Legislation and guidelines have provided many incentives to learn about the value of dead trees. A variety of informational brochures and publications have been made available (Kremsater and Nicholson 1995; Machmer and Steeger 1995; Ministry of Environment, Lands and Parks, and Ministry of Forests 1999; Stevens 1997). Hundreds of forest workers and professionals have received formal training for wildlife/danger tree assessment and riparian management (Forestry Continuing Studies Network of British Columbia: http://www.fcsn.bc.ca). Wildlife trees have been included in public school education programs such as Project WILD (Post and others 1994). Students themselves have created informational software with a wildlife tree and CWD component (Neal and Taylor 1996).

Discussion

The abundance and distribution of dead wood is highly variable and depends largely on disturbance history, stand age, tree species composition, ecosystem type, and decomposition rates. Standing dead trees and CWD will vary in size and stages of decay, even within the same forest. Maintaining the natural variability of dead wood at both the stand and landscape levels needs to be an objective for sustainable forest management. However, there are many real and perceived constraints that make this challenging. Some of the constraints limiting the retention of dead wood in BC's forests are: worker safety (particularly with standing dead trees); logging costs; utilization policy; resistance to change; harvesting techniques; pulpwood markets; salvage initiatives; silvicultural objectives; fuel management; and forest health. Another challenge is defining the natural variability of dead wood, considering the dynamic nature of ecosystems over time and space.

BC's forest management is still mainly concerned with the harvesting of older primary (previously unlogged) forests. These primary forests provide opportunities for management of the dead tree resource that may not be present in second-growth forests established with little consideration for the ecological values of dead trees. Of special concern is the recruitment of large standing dead trees and fresh CWD in second-growth stands. In some instances, most CWD remaining on such sites originated from the first harvest of the primary forest and is therefore large, but usually well-decayed. Where biodiversity is a management objective in second-growth stands, specific strategies, such as direct felling and retention of live stems, will need to be developed to provide for CWD and wildlife trees of all species, size, and decay classes.

Policy has separated the management of wildlife trees and CWD in BC. To a large extent this reflects a lack of specific CWD targets in terms of volume and dimensions. As CWD targets or clearer ecological objectives are developed, it will be important to evaluate how wildlife tree reserves will address long-term CWD input—a current assumption of forest managers. Three main challenges face us. The first is implementation and evaluation of no-cost opportunities for retaining CWD (e.g., minimizing piles). The second is collection of dead wood attributes on both natural and managed stands to provide the necessary background to establish defensible CWD targets that are fully integrated with wildlife tree reserve goals. The third is integration by resource managers of CWD ecological values and management with the traditional view of CWD as salvage, slash, fuel, and waste (Arsenault 2002).

The management and recognition of the dead tree resource in BC has improved since the time when dead trees were left standing only if we could cover their tops with dirt. However, the balancing of dead tree ecological values and timber supply is a challenge still facing BC's forest managers.

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British Columbia's Dangerous Tree Assessment Process[1]

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Abstract

New dangerous tree assessment guidelines have recently been developed by the Wildlife Tree Committee of British Columbia. They are intended to provide information and technical procedures for assessing and safely retaining trees in various situations, ranging from parks and urban/municipal settings to industrial forestry activities and wildland fire fighting. The decision to retain a wildlife tree must include worker and/or public safety, the type of activity occurring around the tree, site factors and tree condition, and wildlife habitat values. These guidelines will be of interest to persons involved in any activity where the management of trees for wildlife habitat or other purposes is desirable.

Introduction

In British Columbia, the historical definition of a standing dead tree or "snag" has been: "*Any standing dead or dying tree over 3 meters in height.*" New Workers' Compensation Board Occupational Health and Safety Regulations (WCB 1998) were adopted into law effective April 15, 1998. With these new regulations, the term snag was replaced with *"dangerous tree."* According to section 26.1 of these regulations, a dangerous tree is now defined as: *"Any tree that is hazardous to workers because of location or lean, physical damage, overhead hazards, deterioration of the limbs, stem or root system, or a combination of these."*

Recently, new dangerous tree assessment guidelines and technical criteria were developed by the Wildlife Tree Committee of British Columbia in conjunction with the changes to the Workers' Compensation Board regulations. The guidelines were first pilot tested throughout British Columbia with a range of individuals experienced

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in occupational health and safety, logging, forest pathology, and forest and wildlife ecology. This information was subsequently incorporated into the provincially sponsored "Wildlife/Danger Tree Assessor's Course" (see WTC 2001), which provides technical information and practical field skills to persons who wish to assess trees for hazards and wildlife habitat value.

Determining Tree Danger

The determination of a tree's failure potential (i.e., the likelihood that all or a portion of a tree will break), and ultimately whether or not it is dangerous, involves a four step process:

Step 1—Determine the level of ground or tree disturbance around the tree

Step 2—Conduct a site assessment overview

Step 3—Conduct a visual tree inspection

Step 4—Make the appropriate safety decision.

Step 1—Level of Disturbance

Various activities are associated with differing levels of ground or tree disturbance. Activities rated as low disturbance, such as surveys, tree pruning, or use of back country hiking trails, involve negligible ground or tree disturbance, and as a result expose people to very little danger. However, as the level of disturbance or exposure increases, such as with timber harvesting, heavy machinery use, or in high-use park facilities, the potential danger and risk of injury also increases. Consequently, potentially dangerous trees considered for retention in these situations must be carefully assessed for any hazards in order to determine tree failure potential and reach an appropriate safety decision.

Step 2—Site Assessment Overview

The determination of a tree's failure potential begins with a site assessment overview, which involves assessing forest health factors (e.g., root rots, insect damage), stand condition (e.g., age, tree species, presence of heart rots), soil profile and condition, and other site variables (e.g., windthrow hazard, slope, fire damage). The site overview provides a context for subsequent assessment of individual trees (i.e., it identifies overall site problems, such as damaged stands or root rot, which can influence tree failure).

Step 3—Visual Tree Inspection

The third step in the dangerous tree assessment process is a visual tree inspection, which results in a failure potential rating (low, medium, or high) for a given tree defect. Failure potential is rated according to tree species groupings, and considers the following factors: hazardous tops, large dead limbs, witches' broom, split trunk, stem damage (scarring, butt rot), thick sloughing bark, fungal fruiting bodies (conks, mushrooms), butt and stem cankers, tree lean, and root condition.

Four native tree species groupings have been identified: Douglas-fir-larch-pines-spruces; western redcedar and yellow cedar; hemlocks and true firs; and deciduous trees ("soft" hardwoods such as aspen, cottonwood, paper birch, maple, alder).

Failure potential ratings for a particular defect, such as stem damage, can be different based on the tree species grouping (e.g., cedars have a larger permissible stem scarring threshold than the other tree species groupings).

With adequate experience and training, the visual tree inspection can be an efficient process that usually requires only a few minutes per tree. If the visual inspection is inconclusive as to the condition of the tree (e.g., root rot is suspected based on the site assessment), a detailed tree assessment can be conducted in order to gather more information on the condition of the bole (stemwood shell thickness) and roots. This involves exploratory tests in the lower bole (e.g., increment boring, drilling, or sounding) and excavating and probing around the root collar.

Step 4—Making a Safety Decision

Once a failure potential rating has been determined from the visual tree inspection, a tree can be rated as either safe (S) or dangerous (D), depending on the level of disturbance or type of activity around the tree. This procedure is illustrated in *table 1.* A classification for coniferous trees is shown in *figure 1.*

Table 1—*Overall Tree Danger Rating.*

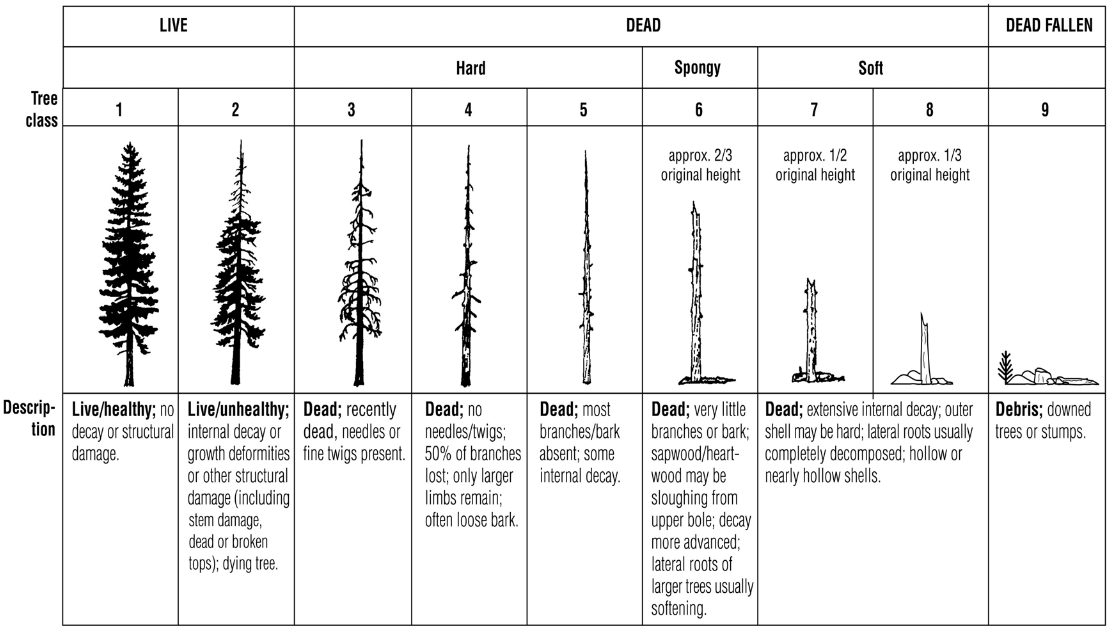
Level of disturbance	**Detection failure potential**		
	Low	**Medium**	**High**
1 (Low)	S[1]	S[1]	S[1]
2 (Medium)	S	S	D
3 (High)	S	S (for veteran and dominant conifers)[2] D (for all other trees)	D
4 (Very High)	S (for class 1 trees) S (for class 2 cedars with low failure potential) S (class 2 and 3 trees with no defects)[3] D (all other trees)	D	D

[1] For Low level (1) disturbance activities, any trees that have one or more of the following significant tree hazards will become D (dangerous):

- Insecurely lodged trees, or hung-up limbs or tops
- Highly decadent or unstable trees (e.g., >50 percent cross-section area stem damage, or >50 percent lateral roots damaged/unsound)
- Trees with recent high lean (>15 percent toward work area or target) and damaged root system/anchoring soil layer.

[2] Employ safe falling and yarding practices around trees assessed as SAFE with Medium failure potential; do not hit or disturb the trees, and fall and yard or skid away.

[3] Trees with no defects will not have any defect indicators other than small dead limbs or minor stem scrapes that are not associated with decay or loss of structural strength. Class 2 trees with no defects will usually be wind- or snow-snapped green trees. Class 3 trees with no defects will usually be insect kill, climate kill, or a recent light intensity fire where no structural tree damage occurred.



	LIVE		DEAD						DEAD FALLEN
			Hard			Spongy	Soft		
Tree class	1	2	3	4	5	6	7	8	9
						approx. 2/3 original height	approx. 1/2 original height	approx. 1/3 original height	
Description	**Live/healthy;** no decay or structural damage.	**Live/unhealthy;** internal decay or growth deformities or other structural damage (including stem damage, dead or broken tops); dying tree.	**Dead;** recently **dead,** needles or fine twigs present.	**Dead;** no needles/twigs; 50% of branches lost; only larger limbs remain; often loose bark.	**Dead;** most branches/bark absent; some internal decay.	**Dead;** very little branches or bark; sapwood/heart-wood may be sloughing from upper bole; decay more advanced; lateral roots of larger trees usually softening.	**Dead;** extensive internal decay; outer shell may be hard; lateral roots usually completely decomposed; hollow or nearly hollow shells.		**Debris;** downed trees or stumps.

Figure 1—British Columbia's Tree Classification System (adapted from Maser and others 1979).

If a tree is determined to be dangerous for a particular type of work activity, then appropriate safety procedures must be implemented. These include removing the tree or any hazardous parts (e.g., top, limbs) or establishing an appropriately sized safe buffer area (called a *no-work* or *hazard zone*) around the tree to eliminate exposure to the hazard. However, if a tree is assessed as safe for a given type of activity, work can proceed up to the tree regardless of whether it is dead or live.

Inherent to the implementation of any safety decision is an understanding of the concept of *"risk." RISK = HAZARD x EXPOSURE*. For example, if there is exposure of workers to a dangerous tree or a *"target"* exists (e.g., buildings or equipment within striking distance of a dangerous tree), then an inherent risk of injury or property damage also exists. On the other hand, if there is no hazard (i.e., the tree is not dangerous) or there is no target exposure, then there is no or very minimal risk.

Applications

Wildlife tree patches and other stand-level reserves (e.g., riparian management areas) are generally the safest and most operationally efficient means of retaining wildlife trees and other biodiversity attributes at the stand level in forestry operations.

However, the new dangerous tree assessment process now facilitates retention of SAFE standing dead and SAFE live defective trees in forest harvesting operations outside of patches and reserves. This is particularly relevant to partial-cutting silvicultural systems, where the retention of individual standing dead and live defective trees is desirable in order to provide additional stand structure, wildlife habitat, and biodiversity values over time.

The dangerous tree assessment process can be applied to a variety of situations, including:

- Forest harvesting
- Silviculture operations such as tree planting and stand tending
- All silvicultural systems, but especially useful for partial-cutting systems such as variable retention, group selection, shelterwood, and single tree selection
- Wildland fire fighting
- Road sides
- Utility corridors
- Parks and recreation sites (e.g., trails, campgrounds and other developed facilities)
- Recreational wooded areas such as golf courses and ski hills.

With these "dangerous tree assessment tools" now available to forest managers, there can be more flexibility in the type, condition, density and location of retained trees in harvest blocks and other applications where the retention of trees is a management objective.

Dangerous Tree Assessment Research and Training

The description and quantification of tree conditions and defects, and the correlation to the likelihood of tree failure, has received relatively little research. There have been a few pioneering studies in this area, however, such as Wagener's assessment of tree hazards in California recreation sites (Wagener 1963). The findings of Wagener's research continue to be broadly applied in North American hazard tree and arboriculture management. Some researchers in the southeastern United States (Smiley and Fraedrich 1992) and in southern California (Matheny and Clark 1991) are relatively active in this field, as are Mattheck and Breloer (1997) in Germany.

In Canada, there is a general lack of research in the field of hazard tree pathology and applied management. However, in British Columbia, a research project has recently been completed (Manning 2001). This project collected quantitative data on visible external tree defects and corresponding internal tree conditions. Correlations were tested between the occurrence of external tree defects and the incidence of internal decay and the resultant loss of stem shell thickness. Highly significant differences ($p<0.001$) were found between the actual/expected stem shell thickness ratios for the three tree defect failure potential ratings (low, medium, high). This suggests a strong positive relationship between the actual shell thickness measured at the corresponding defect positions and the assigned failure potential rating for that defect. For example, where a high failure potential rating was recorded for a defect, such as a stem scar, the corresponding shell thickness at that position was less than the theoretical required shell thickness at the same position. Based on these correlations and related interpretations, the tree failure potential ratings and associated safety procedures used in the "Wildlife/Danger Tree Assessor's Course" (WDTAC) appear to be justifiable and reliable.

The results of this research will ultimately be used to improve dangerous tree assessment procedures and related safety training methods in the WDTAC. Three course modules currently exist for the WDTAC: forest harvesting and silviculture; wildland fire fighting; and parks and recreation sites.

The WDTAC is jointly sponsored by the British Columbia Ministry of Forests, the Workers' Compensation Board of B.C., and the B.C. Ministry of Water, Land and Air Protection. Specific details (e.g., level of disturbance/work activity ratings) and technical procedures associated with the four-step dangerous tree assessment process, as well as additional information about WDTAC modules, can be found on the Wildlife Tree Committee of British Columbia web site: www.for.gov.bc.ca/hfp/wlt/.

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Managing Coarse Woody Debris in British Columbia's Forests: A Cultural Shift for Professional Foresters?[1]

André Arsenault[2]

Abstract

Coarse woody debris (CWD) is recognized as an important component of British Columbia's forest ecosystems linked to biodiversity and ecosystem processes. CWD represents high centers of biological interaction and energy exchange, symbolizing in many ways the complexity of forest ecosystems. Our research on lichens and bryophytes demonstrates that many species are either partially or entirely dependent on CWD. Long-term management of this resource is vital to maintain ecosystem integrity. Previous attempts to recommend province-wide CWD management practices were not successful because of potential increased logging costs and conflicts between utilization standards and recommended CWD volume targets. I demonstrate that small changes to existing forest practices will go a long way in minimizing impacts on the CWD resource without affecting logging costs or access to timber. I propose that a cultural shift in how foresters perceive CWD is a necessary ingredient to improve present practices. This paper promotes such a cultural shift by explaining key CWD management principles and by providing some operational examples.

Introduction

The value of retaining decaying wood in forest ecosystems may be counter-intuitive to many foresters trained in traditional silviculture, which has focused on converting old "decadent" forests into "productive" plantations. The view that decadence (decaying wood) in forests is either undesirable or not necessary has had a profound influence on how foresters and loggers perceive and manage dead wood. A better understanding of the ecological services provided by coarse woody debris (CWD) is essential to initiate sustainable management of this resource.

Many of the ecological services provided by CWD may even help foresters attain some wood production objectives more efficiently and at lower cost. For example, CWD may assist foresters directly with natural tree regeneration by providing safe sites for seedlings (e.g., nurse logs), by protecting seedlings from snowcreep in high-elevation forests, and by reducing trampling damage by livestock in range management areas. Coarse woody debris is also believed to contribute to

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long-term forest productivity (Stevens 1996) by improving soil-moisture retention, contributing to soil structure, maintaining soil stability, and providing nutrient pools.

Long-term forest productivity is obviously linked with timber supply. The contributions of CWD to forest productivity are likely both direct and indirect, resulting from complex interactions among organisms of the detritus food web, the net effect of which is to transfer and transform organic matter, nutrients, and energy from CWD to the forest soils (Harmon and others 1986). In addition to the direct and indirect benefits to wood production, CWD is also an important habitat component for a wide variety of organisms representing the five biological kingdoms. Although the importance of retaining coarse woody debris in managed forests is obvious for a range of values, the development of operational recommendations has not been easy.

The abundance and distribution of coarse woody debris is highly variable in forest ecosystems and depends largely on stand history, stand age, tree species composition, ecosystem type, and decomposition rates. Coarse woody debris will also vary in size and stages of decay even within the same forest. Maintaining the natural variability of deadwood at both the stand and landscape levels is probably a worthy objective for sustainable forest management. However, there are many real and perceived constraints that make the retention of coarse woody debris in forestry operations challenging. Some of the issues that need to be considered when addressing the retention of CWD in British Columbia's forests include: workers' safety, logging costs, maximum utilization policy, resistance to change, harvesting techniques, pulp markets and salvage initiatives, silvicultural objectives, fuel management, range management, and forest health. In addition, the natural variability of coarse woody debris precludes the development of simple or static retention targets, especially considering the dynamic nature of ecosystems over time and space.

In British Columbia, the ecological value of CWD has been recognized within forestry legislation since 1995 (Stone and others 2002). However, the negative perception associated with CWD in traditional forestry and the difficulty of integrating multiple values has made the development and application of CWD management objectives rather challenging. This paper illustrates the ecological importance of CWD with recent research on non-vascular plants, describes briefly the history of CWD management, and provides an overview of a short-term strategy recently adopted in the Kamloops Forest Region to improve the management of CWD.

Non-Vascular Plants and CWD

Non-vascular plants (i.e., lichens and bryophytes) are important organisms in forest ecosystems. These taxa contribute to biological diversity or the many associated ecological processes and constitute critical indicators of environmental change. The importance of coarse woody debris as habitat for certain bryophyte species (particularly hepatics) has been well documented in the literature (Jovet and Jovet 1944, Muhle and Leblanc 1975, Shuster 1949, Soderstrom 1988). The reasons behind the close association between some non-vascular plants and CWD are not fully understood. They probably involve a competitive advantage conferred to these organisms over vascular plants when occupying elevated organic substrates as well as a combination of unique environmental conditions (i.e., substrate moisture, texture, and chemistry), which may be specifically required for some species.

In southern British Columbia several hundred species of lichens, mosses, and hepatics are associated with coarse woody debris. However, only a portion of these species are truly dependent on CWD for their survival. A recent review of the literature and consultations with expert botanists revealed that 16 species of lichens and 23 species of liverworts are strongly dependent on coarse woody debris *(table 1)*.

Table 1—*Preliminary list of hepatics and lichens specializing on coarse woody debris (Godfrey 1977; Goward and others 1994; Goward 1999; Goward, pers. comm.; Schofield, pers. comm.). All of these are considered very strongly dependent on coarse woody debris for survival in the forest. Some are also found on other substrata, but as forest species they are valuable indicators of specific conditions.*

Hepatics

Anastrophyllum hellerianum (Nees) Schust
Bazzania denudata (Torr.) Trev.
Blepharostoma trichophyllum (L.) Dum.
Calypogeia muelleriana (Schiffn.) K. Müll.
Calypogeia azurea Stotler and Crotz
Cephalozia bicuspidata (L.) Dum.
Cephalozia lunulifolia (Dum.) Dum.
Geocalyx graveolens (Schrad.) Nees
Jamesoniella autumnalis (DC.) Steph.
Jungermannia leiantha Grolle
Kurzia makinoana (Steph.) Grolle
Lophocolea bidentata (L.) Dum.
Lophocolea heterophylla (Shrad.) Dum.
Lophozia guttulata (Lindb. Et H. Arn.) Evans
Lophozia incisa (Shrad.) Dum.
Lophozia ventricosa (Dicks) Dum.
Mylia taylorii (Hook.) S. Gray
Odontoschisma denudatum (Nees in Mart.) Dum.
Ptilidium pulcherrimum (G. Web.) Vainio
Riccardia palmata (Hedw.) Carruth.
Riccardia latifrons (Lindb.) Lindb.
Scapania umbrosa (Schrad.) Dum.
Tritomaria excectiformis (Breidl.) Loeske

Lichens

Cladonia borealis S. Stenroos
Cladonia carneola (Fr.) Fr.
Cladonia chlorophea (Sommerf.) Sprengel
Cladonia cornuta (L.) Hoffm.
Cladonia crispata (Ach.) Flotow
Cladonia ecmocyna Leighton
Cladonia furcata (Hudson) Schrader
Cladonia gracilis (L.) Wild.
Cladonia pleurota (Flörke) Schaerer
Cladonia pyxidata (L.) Hoffm.
Cladonia singularis S. Hammer
Microcalicium arenarium (A. Massal.) Tibell
Lobaria retigera (Bory) Trevisan
Nephroma articum (L.) Torss.
Peltigera aphtosa (L.) Wild.
Peltigera britannica (Gyelnik) Holtan-Hartwig & Tønsb.

In Sweden, many species of bryophytes, lichens, fungi, and invertebrates that specialize on decaying wood are in decline (Esseen and others 1992) and some of these species are considered threatened (Berg and others 1994). The decline of log-dwelling hepatic species appears to be the result of both a reduction in large logs and a drier microclimate in managed forests (Soderstrom 1988). At present none of the species of lichens or hepatics specializing on coarse woody debris are considered threatened or in decline in British Columbia, illustrating the critical role B.C. can play in maintaining species at risk globally. This is an obvious incentive for the retention of CWD in managed forests of British Columbia.

Another important consideration from a conservation biology perspective is that on certain sites the number of species dependent on CWD will be higher. For example, in a study of lichen distribution in interior-cedar-hemlock forests of south central British Columbia, Arsenault and Goward (2001) found that over 90 percent of terricolous (ground-dwelling) lichens were associated with elevated woody substrates of which CWD was the most important component. For lichens at least, it appears that the number of species that depend on CWD will increase with increasing soil moisture and snow-depth. The variable level of dependence between non-vascular plants and CWD on different sites probably also applies to other organisms and suggests that CWD retention objectives in managed forests should be site-specific insofar as possible.

Historical Perspective on CWD Management

There have been three main historical periods for CWD management in British Columbia. In the early days of logging low mechanization often meant that only the best wood would be taken out, resulting in considerable amounts of CWD when low quality timber was left on site. This was followed by a period during which clean cut-blocks were considered preferable for silviculture and "fuel management." More recently, with a shift towards an ecosystem management approach, illustrated by the Forest Practices Code of British Columbia, CWD has been recognized as an important value and its retention is required.

Although the present policy calls for the retention of CWD in cutblocks, the perceptions of prescribing foresters and other forestry professionals have not entirely changed from past views. The operational reality of CWD management is further complicated by the diversity of "specialists" involved. Numerous disciplines and issues are involved with CWD management, often measuring it in different ways, referring to it by different names, and even working with different objectives in mind. For example, fire protection officers are concerned with fuel loading, forest ecosystem specialists are concerned with biodiversity, silviculture foresters are concerned with planting spots, harvesting foresters are concerned with logging costs, and scaling foresters are concerned with utilization standards.

CWD management has been the subject of heated debate ever since the implementation of the Forest Practices Code. The approach of using specific CWD targets within the biodiversity guidebook (Ministry of Forests and BC Environment 1995a) was delayed in 1995 as a result of a potential conflict between the timber utilization policy (e.g., zero waste policy) and CWD retention targets. Since then, several attempts to reach a consensus on CWD management have been unsuccessful. In the interim the timber utilization standards take priority over CWD retention. The result is that CWD management is presently focused on the retention of uneconomic wood. In addition, companies can leave a small amount of green sawlogs behind without being billed for waste but are charged volume against the annual allowable cut.

Towards a CWD Management Strategy

Despite the lack of specific CWD management guidelines, foresters are still required to set CWD management objectives in forest development plans and silvicultural prescriptions. In addition, foresters also have to balance CWD management with other potentially competing stand management objectives such as stocking standards, range, and fuel management. In order to provide better guidance for CWD management, the Kamloops Forest Region recently developed a short-term strategy for CWD management. The general approach of the strategy is to clarify the policy and legislation pertaining to CWD management, providing prescribing foresters key information to assist in managing CWD. The focus of the strategy is educational, i.e., to provide CWD management guiding principles, planning and prescription considerations, and CWD management tips. The strategy will be implemented for a period of three years, during which monitoring programs will be used to assess its efficacy.

Guiding Principles for CWD Management

In order to assist prescribing foresters in the development of CWD management objectives in forest developments and silviculture prescriptions, the following key guiding principles have been developed. In general these principles will help foresters avoid wasteful practices, encourage an integrated management approach and promote the maintenance of variability across the landscape.

- CWD accumulations, especially on landings and roadsides, should be minimized, bearing in mind that some accumulations will be inevitable for reasons of safety and operations. Some small CWD piles dispersed in cutblocks may be necessary to provide valuable habitat for some mammals.
- Larger pieces of CWD are more valuable than smaller pieces—they last longer, hold more moisture, are useable structures for a greater number of organisms and cannot be easily replaced.
- Ecologically, it is advantageous to maintain the full range of decay and diameter classes of CWD on every site—different functions and ecosystem processes require CWD in different stages of decay.
- Coniferous material decays much more slowly than deciduous material and therefore remains part of the useable structure of a stand for a much longer period of time. However, the faster decay rate of deciduous CWD also provides significant short-term ecological benefits. Retention of a diversity of species is advantageous.
- CWD can be managed in conjunction with wildlife trees and other constrained or reserve areas. Standing live and dead trees and/or stubs retained on cutblocks represent important sources of CWD recruitment.
- CWD has additional value in riparian areas, which are a valuable habitat resource for many species of wildlife. CWD entering or falling across a

stream produces habitat for fish, invertebrates, and vegetation. Most importantly, it contributes to stream geomorphology. However, excessive amounts of woody debris can have negative effects on stream biology.

- The composition and arrangement of CWD should be managed within acceptable levels of risk of wildfire, insect pest, and forest disease outbreaks.
- The retention of CWD should be harmonized with all other silvicultural objectives.
- Variability in the levels of CWD should be maintained at the landscape level. The natural distribution and amounts of CWD will vary according to biogeoclimatic gradients, stand types, and stand development history. Although the natural distribution of CWD cannot be mimicked exactly, it is important that CWD management capture landscape variation and site-specific variations through different management practices.

Sources of CWD

In many cases, logs already lying on the forest floor will be left after harvesting. This constitutes an obvious source of CWD. In addition, all other uneconomic wood resulting from harvesting (such as breakage, short pieces, tops, and low-grade timber) also provides existing sources of CWD. When the intent is to leave these behind as CWD, efforts should be made not to damage them during harvesting operations.

Ensuring that large pieces of CWD will be maintained through several rotations will be a challenge. It would be wise to plan ahead and identify “low cost sources” of CWD recruitment. Long-term CWD recruitment may be addressed by leaving reserves and wildlife trees, possibly including cull trees. “Stubbing” (leaving high stumps, often several meters in height) may be used to complement these reserves, particularly when there are few wildlife retained trees or when wildlife trees are restricted to portions of the cutblock.

CWD and Risk Management

The risk of bark beetle activity should be evaluated where wildlife trees blow down or if many large live trees are felled and left in place. If fallen trees are near an existing infestation, preventative actions may need to be taken, particularly with Douglas-fir and spruce. The actions will depend on the risk of spread of bark beetles, the value of the timber, the value of the CWD, and the impact of different actions to the standing trees. The level of risk to timber is determined by the probability of bark beetle damage (based on the susceptibility of the stand and the proximity of existing beetle infestations). The bark beetle management guidebook provides further information on hazard and risk rating criteria (Ministry of Forests and B.C. Environment 1995b).

Fuel management plans are no longer required under the Forest Practices Code. However, the Forest Fire Prevention and Suppression Regulation states that a person who, on Crown or private land that is in a Tree Farm Licence or a Woodlot Licence, harvests timber or carries out a prescribed activity must assess the fire hazard existing on that land. Fine fuels, i.e. pieces less than 7.5cm in diameter, pose the primary fire hazard associated with woody debris. Prescribed burning, under the appropriate conditions, can remove these fine fuels and have minimal impact on CWD.

CWD Management and Salvage Operations

When stands affected by catastrophic disturbances (e.g., wildfires, windthrow, bark beetle infestations) are salvaged, efforts should be made to ensure a good distribution of CWD over the area. Care is necessary when contemplating salvage operations within wildlife tree reserves or riparian buffers. In cases where salvage is required for risk management, consideration should be given to designating an equivalent replacement area. It may be possible to retain incidental windthrow in sensitive ecosystems such as riparian areas and wildlife tree patches (WTPs) for long term CWD. The Small-scale Salvage Program removes standing dead and downed trees from harvested areas. The recovery of this material poses a potential risk to the biodiversity values provided by wildlife trees and CWD. However, the integration of CWD management within forest district procedures for small-scale salvage will help minimize this risk. These procedures may include: identification of areas of access and operation; designation of high value habitat; instructions concerning salvage from sensitive ecosystems such as WTPs and riparian management zones (RMZs); information on CWD and wildlife tree values; and safety concerns.

CWD and Silviculture Activities

Management of harvest and post-harvest activities should minimize adverse impacts on CWD. The main objectives are to avoid piling CWD, avoid damaging CWD with heavy machinery or broadcast burning, and plan stand-tending activities to ensure some CWD recruitment.

In some special circumstances it may be appropriate to modify stocking standards to meet CWD objectives due to debris accumulation and reduction of plantable spots. Options include: modifying target-stocking levels; modifying the minimum allowable distance between trees; and utilizing clumped planting patterns.

CWD Management Field Tips

The following field tips have been employed to manage CWD in different parts of the province. They are not necessarily applicable to all situations but provide several options and perhaps a template, which foresters can use to innovate and develop other solutions that would be suitable to specific situations.

- Bucking on site: An approach to avoid CWD accumulations on landings is to buck on the site rather than at the landing. This approach can be applied over the whole cutblock or over a portion of it.
- Delimbing and topping: Where whole tree harvesting is carried out, CWD levels can be increased by delimbing and topping on site rather than at landings and roadsides.
- Leaving cull trees standing: Trees (live or dead) that have obvious defects are often referred to as cull trees and will usually produce low-grade lumber. In many cases the costs of harvesting and manufacturing outweigh any economic gain, making cull trees ideal candidates for long-term CWD recruitment. Identifying cull trees during operations as potential sources of CWD is a good example of improving CWD management and reducing logging costs. The major types of defects are forks, multiple tops, spiral grain, extensive rot, insect damage, and scars of various kinds.

- Avoiding yarding of uneconomic wood to landings and roadsides: Yarding uneconomic wood to landings and roadsides reduces its ecological and habitat values and can add costs. In addition, it may be expensive and time-consuming to redistribute this material back onto the site.
- Reducing the number of empty trips: Redistributing CWD has been successful in blocks with very little initial CWD volume. When the burning of cull and debris piles is eliminated or lessened, costs may be reduced. Licensees will want to determine if the redistribution of uneconomic wood should be done over the entire cutblock or only on a portion of it. To help facilitate the redistribution of uneconomic wood back onto the cutblock, the bucker might be able to place pieces of uneconomic wood in a pile easily accessible to the skidder. As the skidder comes to the landing, the operator will be able to release a load of incoming logs, grab a turn of uneconomic wood and return it to the cutblock. The general approach of returning uneconomic wood during operations can also be used in conjunction with some grapple yarding operations where safety considerations and terrain permit. Communication with the yarding crew to identify uneconomic wood is an efficient means of improving CWD retention on the site.

Red Flags

Although a detailed assessment of CWD management in the field has yet to be conducted, it is clear that certain sites deserve close attention. For example, we already know of at least three specific situations that may become problematic:

- Observations in second harvest stands of coastal temperate rainforests suggest very few large pieces of CWD be left behind.
- Some young thrifty stands being harvested in the southern interior of British Columbia have very little decay and leave few opportunities for CWD retention within the present policy framework.
- In dry forests, prescribed burning often eliminates large pieces of CWD in the advanced decay stages. Although it is not a widespread practice at this time, renewed interest in the application of prescribed burning in these forests may pose a serious threat to species dependent on well-decayed logs and stumps.

Assessing CWD management in the field over the next 3 years will help to identify other problem areas and make improvements to the CWD management strategy.

Conclusion

The short-term CWD management strategy proposed by the Kamloops Forest Region should assist in minimizing the impact of harvesting on the CWD resource and will provide baseline information helpful in the development of more specific guidance. Although there is interest in developing CWD volume retention targets, it is not clear that this will necessarily translate into "better" CWD management. One of the key ingredients to achieving this end is to help professional foresters to develop an understanding of the ecological value of CWD and its role in the ecosystem. For some, this may involve a profound cultural shift because the CWD resource, often known as slash, waste, fuel has been perceived as a problem for a very long time. Addressing the many conflicting forest management objectives that deal directly or indirectly with CWD is a perfect example of integrated forest management in action, and will no doubt continue to generate a great deal of interest and debate.

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Water, Wildlife, Recreation, Timber… Coarse Woody Debris?[1]

John R. Mount[2]

Abstract

A natural forest ecosystem has two essential components that seem to be in conflict with one another: fire and coarse woody debris. If fire originally occurred at regular intervals with each acre burning every 10 years, then how could coarse woody debris have existed? As a part of my management program, I advocate returning the forest to a natural fire regime. I also understand that woody debris in all of its forms is required for a healthy forest ecosystem. Given this, I needed additional information on how these two diametrically opposed components existed together in the central Sierra Nevada. After 20 years of harvesting timber and using prescribed burns, I have determined through an inventory system that coarse woody debris and fire can and do co-exist.

Introduction

Before 1980, Southern California Edison Company lands were in a condition that was less than any desired level as a functioning natural ecosystem. A patchwork of brush fields, under-stocked areas, and overstocked stands was the vegetative pattern of the lands at that time. This forest composition was a direct result of the harvesting methods used at the turn of the century. The large brush fields replaced harvested old-growth stands, and the overstocked stands consisted of young, untouched stands that had no value to the land managers in those early years.

Fire exclusion has also significantly skewed the vegetative structure in all of the various stand types. There was too much woody debris in all size classes of dead material, with the exception of very large snags. Although there was an abundance of large downed material, (logs over 40 inches) most of it was over 50 years old and in an advanced state of decay. All of these factors contributed to the disrupted, unhealthy forest that I would be managing.

In 1980, I wrote a Land Management Plan for my new employer, Southern California Edison Company. As I was outlining my vision of a well-managed forest, a conflict between natural fire and coarse woody debris surfaced. I knew both were significant to the forest ecosystem, but they seemed mutually exclusive. Because my long-range goal was to return the property to a pre-1850 stand structure, the challenge was to both maintain a healthy forest ecosystem and affect the needed changes within the boundaries of the biome of this area. The very first priorities were that I needed to harvest the over crowded stands that occupied 50 percent of the

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property, and at the same time, return fire to the ecosystem. I also needed to consider tree species distribution and how to restore it to pre-1850 conditions.

Early objectives included reduce fuel loading and stocking, restock brush fields, and maintain an adequate amount of dead material. In other words, the primary management objective for coarse woody debris was to preserve an adequate inventory of material that best suited wildlife needs, while also reducing forest fuels. My approach had to be fairly rapid and economical. It became apparent that more detailed information was needed about the stand structure. The information was necessary not only for timber production but also for other components of a balanced forest ecosystem. There were several obvious deficiencies, such as large snags and snag recruitment, larger size trees, and overstocked areas of young trees (less than 20 feet in height). However, hard data was lacking.

Methods

The first step to understanding the co-existing relationship between coarse woody debris and fire was gathering information. In 1993 I was finally able to establish a forest inventory system. The availability of geographic information systems (GIS) and global positioning systems (GPS) made it possible to include a large variety of information and growth modeling of the existing forest composition. The inventory system that was designed included data on brush species, oaks, snags, and coarse woody debris as well as timber volume and species distribution.

The field portion of the inventory system used 1/10-acre circular plots. The small plot size was used so that more points were sampled with relative uniformity within each plot. With larger plot sizes, a large variation exists within each plot in terms of canopy cover, brush percentage, or stand type. Using the smaller area size encourages variety while maintaining consistency among measurements. Also, the measurements of coarse woody debris include a breakdown of dead and downed material, as well as snag classification. I divided the measurements into size and decomposition levels as expressed by age classifications.

Another category was added to the inventory system termed “green snag.” A green snag was defined as a live tree that would not be harvested due to disease or deformity, but would be preserved for wildlife purposes. At this time, there was an obvious deficiency in the existing stand structure of unhealthy trees. Because the forest was relatively young, I needed to increase the number of trees that for one reason or another were dying or damaged. I would mark these “wildlife” trees with a “W,” but needed an estimate of size and volume. A “W” is also used for other reasons such as nesting trees, perch trees, potential habitat trees, as well as green snags.

Before the collection of any hard data in 1993 the program needed to proceed in 1980. Timber harvesting is one method of increasing coarse woody debris. High stumps (10-15 feet), tops, cull and sound logs, snag, and green snag retention all contribute to the inventory of debris. The opposite is true for salvage logging. In my management program, I have made every effort to reduce or eliminate salvage logging in order to help maintain woody debris. In fact the only salvage logging I have done on these lands was conducted in 1991, during the drought. Even during those operations, only very recently killed trees or trees actually infested with the bark beetles *(dendroctonus brevicomus* and *monticoli)* were removed. Edison has experienced far less infestation than surrounding forest lands due to harvesting in the first 10 years (1980-90). The most difficult choices in both of these salvage operations and current harvesting is leaving recent snags that have merchantable value.

Although I have an active coarse woody debris management objective, I have an even more active fire management program. After studying all available information on natural fires that burned in the Sierra prior to 1850, I learned that they did not burn only with low intensity, as many people seem to believe. Even many catastrophic fires of today burn in a patchwork manner, leaving many completely unburned islands within denuded areas. Natural fire, as a result of a reduction of fuels, burned for many days and even months and burned hot as well as with low intensity.

The burning that I practice duplicates these fires. Initial entry is done under conditions that only burn lighter fuels, usually less than 4 inches. Subsequent burning allows us to burn very hot in areas that are adjacent to unburned patches. This burn pattern allows for areas of high coarse woody debris inventory with open areas intertwined.

Results

The results of the burn program overlaid with the coarse woody debris retention goals have been better than expected. Using available research data as a base, the inventory indicates above-adequate volumes of coarse woody debris scattered over the entire property. The breaking up of the forest structure and occurrence of coarse woody debris also allows better fuels management against large fire incidences. The key is how the burning is done.

More directly, inventory results show an adequate stocking of coarse woody debris over the areas treated by fire. Most importantly, these areas are neither continuous nor contiguous with each other and are surrounded by openings with no woody debris at all. Snag inventory and recruitment numbers are above most recommended thresholds and increasing. The firm policy of not salvaging any dying tree except for those hazardous to the public has increased numbers of snags. The initial burning in a new area has been limited to the reduction of light fuels (less than 4 inches in diameter). Subsequent burning has been done in such a manner as to create the pattern of patchy occurrences of course woody debris. Bird surveys support the conclusions that fire has not reduced the incidences of any species after the initial burning. Subsequent hotter burns indicate short-term differences followed by increases in both richness and diversity.

Discussion

By introducing fire under a variety of conditions, the results of each burn are different and important. Because of this fact, there are no unsuccessful burns. More importantly, by understanding fire behavior, certain desired results can be achieved. I have been successful in many respects, including the increase of deer browse, creating conditions conducive for natural reproduction, thinning of these new stands, rejuvenating vegetation types such as willow, creating small openings, increasing coarse woody debris, increasing wildlife diversity, and reducing fire hazard. In fact, due to the many legal obstructions that are reducing prescribed burning opportunities, the only problem may be that there is too much coarse woody debris.

The initial process of stem reduction was completed in about 15 years. The conversion to the proper species and size composition is ongoing and will take about 30 more years. There is still a long way to go before I know which variables and components to watch in order to determine ecosystem health.

Where do I go from here? Research is paramount in knowing how to manage the forests in the future. However, the overwhelming data and sometimes contradictory research findings must be carefully evaluated. There is some good in each research project, though one can also find much misleading information. These apparent conflicts are due to varied locations of the research projects as well as their differing objectives. There is also much personal bias, not only in the data but also in turf wars between researchers.

Monitoring the work is obviously a requirement to determine the program's progress. This alone is a major focus of our program, with continuous debate on cost effectiveness. What needs monitoring and how it should be done is one of the most time consuming (and fun) discussions that my staff has each year. Relevancy, costs, and amount of detail required are some of the issues that are argued. Currently, some of our monitoring projects include bird surveys, deer counts, brush growth, tree spacing, stand release, competition, hardwood physiology, and effects of fire on the ecosystem.

Reconciliation of the differences between research and monitoring efforts is also required before work plans can be initiated in a particular ecosystem. This is mainly due to the lack of research done on this subject and also lack of knowledge on unaltered forest ecosystems. In the future, research will determine numbers of snags per acre and how many tons of coarse woody debris is necessary for a healthy forest. Unfortunately, there will be many changes in those results and numerous arguments will ensue before any final knowledge is ascertained. Grandiose programs initiated in Washington D.C. or Sacramento that may protect a single species is not the answer. Natural systems are resilient and most do not require expensive and time consuming plans to help them along. As land managers, we must understand the naturally occurring cycles and manage within them. We should then use those tools that natural systems have provided, such as fire. As a resource component, fire should be used as a determinant for the proper amount of coarse woody debris.

Creating and Maintaining Wildlife, Insect, and Fish Habitat Structures in Dead Wood[1]

Timothy K. Brown[2]

Abstract
Dead wood is an important component of the forest for many species. In many locations, however, the presence of dead wood has declined, and there is a need to make what is left more suitable for the myriad of creatures dependent on this material. In this paper, I will summarize the value of dead wood for these species and describe methods for improving the dead wood component of the forest to meet the needs of a variety of vertebrates and invertebrates.

Creating Wildlife Habitat Structures in Snags, Logs, and Stumps

In forested ecosystems, habitat diversity is directly related to tree form diversity. Snags are trees, dead or living (living snags are live trees with dead sections) that have been killed or altered by disease, lightning strikes, and wind. Each snag is unique since various factors, such as age, species, location, and cause of mortality or alteration, characterize each snag differently.

Snags (standing or downed trees) and other forms of dead or unmerchantable woody structures are recognized by many land managers to benefit wildlife and other biota on forested lands. At least 96 vertebrate species are associated with snags found in forests of Washington and Oregon (Rose and others 2001). A large proportion of forest-associated bird and mammal species require cavities to live in, many provided by snags or other forms of woody debris in various stages of decay. Thomas and others (1979) documented 62 wildlife cavity users in montane forests of northeast Oregon and southeast Washington. To other landowners, snags may represent unclaimed firewood, lightning rods, fire hazard, or loss of potential timber commodity. Many political jurisdictions have forest practice rules or policies requiring prescriptions to retain snags or designate green trees for future snag recruitment in managed landscapes. Wildlife habitat prescriptions, whether they are scientifically based or not, that are implemented and monitored may provide more habitat management options in the future and a more positive effect to increase species diversity and/or abundance as the forest matures.

Both dead and living snags are important and offer somewhat different habitats. For example, living snags that retain some lower branches below a sturdy, bare trunk or spike provide ideal protection and support for large predatory birds such as hawks

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and eagles. When a snag is formed abruptly, for example, by wind or lightning, the damaged tissue is quickly colonized by insects and fungi, which in turn provide meals for primary excavators such as woodpeckers and predatory insects. Secondary cavity users such as owls, chickadees, swifts, bats, and bees extend the usefulness of the snag modified by primary excavators. Flaps of loose bark, hollows, and crevices often found in snags are favored bat roosting sites (Tim Brown, pers. obs.).

As the snag decomposes and falls to the ground, it will provide shelter, dens and runways for a variety of small mammals and amphibians. Hollow tree trunks, either in the partially standing snag or the downed trunk, creates protective habitat for denning martens *(Martes americana),* fisher *(M. pennanti),* coyote *(Canis latrans),* and raccoon *(Procyon lotor).* Shrew-moles *(Neurotrichus gibbsii),* shrews (*Sorex sp.*), deer mice *(Peromyscus maniculatus),* salamanders, and frogs may use smaller cavities in the decaying wood for thermal and protective cover, in addition to foraging on the various insect larvae harbored there. Small mammals can act as dispersing carriers for fungi, and if they are using a down log as a runway, their feces deposit fungi, which in turn, recycle nutrients to the soil. The “dead wood” on the ground is a storehouse of energy and nutrients. The decay of this debris steadily contributes to the organic layer of the soil. This organic soil is critical to establishing a fertile medium for supporting a diverse ecosystem of plants, small mammals, amphibians, and invertebrates.

The purpose of this paper is to review techniques that I have experimented with in the last 30 years. As a former professional timber industry tree faller, forest firefighter, and owner and operator of a tree-service company, I have witnessed a plethora of wildlife using wood habitat, such as cavities, broken tree-tops, and deep fissures of lightning-struck trees. From these observations, my goal was to create similar habitats using chainsaw and drills. On trees and standing snags, many of the enhancements were performed aboveground anywhere from 2 m to as high as 30 m or more. Although most of the methods described in this paper were employed in the Pacific Northwest, these enhancements should work in other temperate conifer and hardwood forests of the U.S. and overseas. Land managers and their biologists can likely employ most of these techniques presented in this paper by considering the specific type, size, and location of the alteration for the particular target species of their area.

Wood Habitat Planning and Retention

With skill and planning, forest management activities and wildfires resulting in wildlife habitat loss may be managed to reduce further impact to wood habitat. In all likelihood it will be necessary to prioritize the efforts devoted for snag or other habitat preservation. The following are criteria useful for selection of elements of the landscape to be retained or managed:

- Trees or snags with trunks of 30 or more centimeters DBH
- Snags providing sites for platform nests
- Snags with obvious wildlife holes
- Snags with hollows
- Snags with conks (indicating soft decay is underway)

- Downed trees with hollows.

To retain snags in proposed logging operation sites, no harvest or no-work zones can be established around designated snag-retention areas. In a forest fire situation, crews, at their discretion, can reduce the potential hazard posed by these trees by routing fire trails around them and establishing no-work zones around each snag. These zones should cover an area with a radius of 1.5 times the height of the snag.

The hazard zone can be reduced to acceptable limits by topping threatening snags. Criteria and procedures for any topping should be introduced by the biologist/ecologist of the land management entity and incorporated into the sale administration process. Safety regulatory agencies should participate with the land managers to review topping prescriptions. Topping prescriptions, as well as other restoration techniques, may vary within a planning area depending on, for example, existing stand conditions, snag species, and proposed tree harvest methods. Holistic forest management planning is especially important to foster long-term stand and landscape conditions for wildlife species and other biota associated with snag and down wood habitat.

It is apparent that the same features that make the snag an asset for wildlife habitat may be a liability for the forest worker or visitor. Signs of a hazardous tree may include:

- A significant lean
- A broken top and/or branches that are hanging up in the tree
- Snags with hollows
- Root or other disease (noted by needle discolor, poor cone production, etc.)
- Advanced decay into the bole of the tree
- Visible cracks or hollows in the bole of the tree
- Visible wildlife excavations
- Loose bark
- Length of time that the snag has been dead or tree stressed
- Lightning scars.

In forest fire situations the possibility of the snag serving as a “fire ladder” that may spread the fire into the canopy can be reduced by removal of low hanging and dead branches from the lower portions of the tree. Snags can be protected by removing fine litter and woody undergrowth at its base, thereby eliminating material that could fuel the fire near the snag.

Ultimately, the safety of the crew takes precedence over maintaining wildlife habitat. If, for example, establishing a “no-work zone” around a potentially hazardous snag is not an option, or if a combination of dangerous features, such as degree of lean and amount of decay, are significant, then worker safety requires removal of the snag. If a snag must be felled, it may still provide valuable habitat. Large, downed hollow or partially hollow logs are among the slowest habitat elements to be replaced after harvest or fires. Hollow logs may be homes for returning marten, fisher, lynx *(Lynx canadensis),* bobcat *(L. rufus),* bear (*Ursus* spp.), raccoon, and numerous other creatures.

Specific Habitat Creation Techniques

Hollow Trees

Hollow trees provide the basic ingredient for a blue-ribbon wildlife tree. In the Pacific Northwest, for example, tree species such as western red cedar *(Thuja plicata)* or Douglas-fir *(Psuedotsuga menziesii)* at least 60 cm in diameter should be checked for hollowness with a sounding ax. A hollow tree will emit a lower sound when struck than a solid tree. An increment borer can be used to determine whether the tree is indeed hollow and the extensiveness of the cavity. Once a hollow tree has been located, the worker should check to ensure that existing fissures or cracks provide entry to the hollow. If there is no suitable entrance, a quick drill with a chainsaw may permit access. Bats will enter a hollow tree from all levels, including open root areas that lead up into the tree trunk. However, a 9-meter (30 feet) or higher entrance hole is desired because it provides enough drop space for the young as they launch their first flights.

Locations for entrance holes should be selected carefully. Enlarging an existing partial opening or placing the hole in an already existing dead area, such as a dead branch stub are good places. The opening should be free of obstructions for safe egress and ingress. The opening should also be placed at a 20-degree angle upward from the horizontal. This angle helps keep the interior warm and provides a measure of safety from predators.

Bat Roosting Slits

On standing trees and snags these installations combine the close quarters and large surface areas that bats use. They serve as bat apartment houses and provide a dry, warm pocket for roosting or possibly nurse colonies. For a multiple slit dwelling, an entry port about 20 cm by 30 cm (8 inches high by 12 inches) long is excavated in the side of the tree. After the entry port is excavated, the slits are cut up into the interior of the tree as vertically as possible. Two to three separate slits may lead off from a single entry port. Alternatively, separate entry ports for each slit may be excavated. If the selected tree is green, it will be necessary to cut away the bark around the entry ports to prevent their closure by heal-over from cambium growth. It is also important to cut the cambium away to prevent oozing sap from sticking to the bats' fur and causing flight problems, or perhaps, avoidance of the site because of the presence of oozing sap.

Bat Bark Flange

A magnificent old Douglas-fir tree typically has bark at least 15 cm (6 inches) thick, with many vertically running fissures or crevices up to 15 cm deep and several meters long. The crevices in large-diameter (i.e., > 76 cm) Douglas-fir, or other species with deep fissures, provide abundant niches for forest bats. Solitary male bats use these crevices extensively. Smaller-diameter Douglas-firs (< 51 cm) have not developed the thick-fissured bark, and management of early seral forests for habitat restoration requires an innovative approach for creating surrogates for bark crevices.

To install bark flanges, tangential cuts should be made upwards about 25 cm (10 inches) on the side of a tree trunk. The depth of the cut should be just through the bark with only enough wood to provide a stable flange. Wedge a 19 mm (¾-inch) diameter piece of wood up into the top of the flange to keep it open.

Bat Girdle Flange

A tree that has been selected for killing by girdling can be utilized as bat habitat while the tree is dying. The girdle is designed with multiple collars or flanges 20 to 25 cm long around the circumference of the tree and hanging down over the shaved-off portion of the girdle. Bats will be attracted to the underside of these flanges. For convenience, the bat girdle flange may be placed at breast height (1.4 m above the ground). Tree girdled at this height can be expected to remain erect for 20 or more years, and the girdle needs to be installed 6 m (20 feet) off the ground. This increased longevity is worth the trouble of tree-climbing in most cases.

Bat Stumps

Usually a second growth forest has stumps left over from the preceding forest. These old, large-diameter (> 76 cm) stumps are particularly valuable habitat and even smaller stumps can be used to enrich the habitat. The tallest stumps are most suitable for bat stumps. A chainsaw can be used like a drill to bore out a tunnel through the stump. The tunnel should be no wider than 19 mm (about twice the kerf width of the bar) and at least 20 cm (8 inches) from the top of the stump to keep the interior dry. Bats will use these artificial hollows for roosting.

Sapwells

Sapsuckers create sap wells in the bark of coniferous and deciduous trees and shrubs. Sap is an important seasonal component in the diet of these birds. Sapwells are often used by other birds such as chickadees, hummingbirds, warblers, and nuthatches. Squirrels and chipmunks also exploit sapwells. Sapwells can be installed with a chainsaw by lightly touching the trunk of a tree with a small chainsaw or drill. The bark is barely opened up to the cambium, not into the wood. The best time for sapwell construction is in the early spring, when the cambium is rapidly producing new phloem. Sapwells can be placed at all levels in live trees, but levels 5 m (15 feet) or greater seem to be preferred.

Lightning Strikes

In late-successional forests in the western Cascade Mountains in Washington, many of the tallest surviving trees have been struck by lightning at some time but have not burned significantly. If the strike was fairly recent, an irregular charred line that runs down the vertical length of the tree should be obvious, but often evidence of a lightning strike is not visible. Visible damage to the tree trunks may include superficial bark flaking to strip like furrowing along the trunk. Often the tree tops have been shattered and lost, and a spiral scar with a crack along its axis winds around the trunk. Most have shallow continuous scars 15 to 127 mm (0.6 to 5.0 inches) wide along their trunks. The average scar extends along 80 percent of the tree height, often to the ground level (Taylor 1969).

Lightning strikes expose the cambium of the trees to insect activity that provides a bountiful and convenient food source for insectivores. Fungi may enter at splits and deep openings made by lightning and begin the process of sapwood and heartwood rots. Birds also can readily use the lightning-induced crevices as points to initiate excavation. Conner (1975) noted that some lightning-created snags were used by cavity-nesting birds. Bats find temporary roosting sites along the strike crevices. Since lightning struck trees are usually poor quality for timber, they should be retained on the landscape as wildlife trees. The structure of a lightning strike can be mimicked by installing a long vertical slit down the trunk of the tree. Strikes often travel straight down for some distance but then curve off center nearer the base of the tree. Artificial lightning strikes should be installed in this asymmetric way and can be installed in either dead or living trees.

Raptor Perches

"Healthy" second-growth forests that open along rivers and lakes may be lush-looking, but provide marginal perch habitat for eagles and other large-bodied raptors. Bald eagles *(Haliaeetus leucocephalus),* for example, need lookouts and towers from which to locate prey and to begin their hunt. Typically, early-seral hardwood forests, such as small-diameter (< 30 cm) red alder *(Alnus rubra)* and black cottonwood *(Populus trichocarpa),* are densely branched and not useful as raptor perches. However, branches in dense crowns can be thinned to create raptor perches. Trees along a river in a fairly open location may be improved for use by eagles by thinning and girdling branches to provide visibility and convenient perch sites. When pruning, branches in the lower third of the trees are removed and those in the upper two-thirds of the trees are thinned.

Mammal Dens

Most of our forest mammals use some sort of cavity for denning. Insectivorous small mammals, such as shrews (*Sorex* spp.), shrew-moles, and deer mice, are known to exploit log or stump cavities for den sites and runways. Larger carnivorous mammals, such as members of the weasel family, use hollow logs or hollow trees as den sites. Maintenance or creation of some of these den structures can facilitate use by these creatures.

Habitat Logs

Dens can be constructed in logs of all sizes. Windthrown logs suspended above the ground are ideal, because they remain drier longer than logs flush with the surface of the soil. With a chainsaw, selected log should be cut laterally to create two halves, then sliced at the end of the cut to release the upper half. A den of the target species can be cut, contingent upon log size. An entrance hole just large enough for the target species should be placed along the side of the cut. The lid on top of the log should be secured with nails or cable.

Jagged Top Snags

A jagged top snag will collect a greater number of fungal spores to begin the decay process. Irregularities in the bole will collect precipitation and fungal spores and appear more natural. To "naturalize" a snag, a portion of the top of the newly topped tree should be sliced at an angle. Then the top of the snag should be cut to create crevices in the top. Finally, the saw should be "bounced" on the top to create a number of incisions.

Improvement of Aquatic Habitats for Wildlife

Urban development and past management of forests along streams, wetlands, and lakes, have reduced the presence of large dead trees that historically fell into these wet areas. Introducing wood habitat to lotic ecosystems, for example, may require extensive and expensive restoration efforts and may conflict with social, political, and scientific efforts to protect Federal-listed salmonids, especially in regions within the Pacific Northwest.

If restoration is practical, especially in urban areas with lentic habitats, re-introducing wood habitat will likely benefit invertebrate and vertebrate species and associated biota where future recruitment of wood is unlikely to occur. Adding woody debris directly in water and adjacent uplands can increase amphibian productivity, for example. Observations show that placement of thin-stemmed woody vegetation in the water provides egg oviposition sites for the northwestern salamander (Richter and Roughgarden 1998). And water temperatures are crucial for the proper development of amphibian egg masses. Areas shaded from direct sunlight may not provide appropriate temperatures for quick development of amphibian egg masses compared with portions of lakes exposed to sunlight for longer periods. So when providing structures designed to provide support for amphibian egg masses, one should prioritize areas with warmer water due to longer duration of sunlight. Other species of native amphibians, such as the red-legged frog, may also loosely secure their egg masses to woody stems. Such woody material would float up and down with the water level fluctuations, preventing desiccation during water level changes. Aquatic amphibians spend a good deal of time in upland habitats. Addition of large woody debris to upland areas enhances amphibian overwintering opportunities.

Waterfowl, amphibians, turtles, and riparian-associated wildlife are attracted to open bodies of water, and the presence of logs associated with open water areas increases the quality of the habitat for such species. In open bodies of water, a mixture of loafing logs for waterfowl, otter, and turtles should be placed to maximize use by individual wildlife species. Addition of logs to the area of ponds and lakes receiving the greatest amount of daylight provide basking sites for turtles so that they can more quickly increase their body temperature in a secure location. Waterfowl roost safely on secured logs in the water, and several mammals use floating logs, including mink *(Mustela vison),* river otter *(Lutra canadensis),* and beaver *(Castor canadensis).*

Maintenance and Improvement of Snags and Logs for Pollinating and Predator Insects

Predaceous and pollinating insects, such as ants, wasps, bees, and ladybugs, contribute to forest health and productivity. Taxa including ants and ladybugs prey on a number of forest insect pests. Solitary and colonial bees pollinate a variety of flowers and berry-producing shrubs.

Many of these insects use snags and downed woody debris for many of their life activities. Some are primary cavity excavators, such as beetles and ants, that create cavities in dead wood for rearing their young. Many insects are opportunistic and use cavities of all kinds, including those created by wood rotting fungi, for their own reproduction or for overwintering habitat. Special structures and installations for pollinating and predaceous insects in standing and downed wood materials may be created by various mechanical means. Galleries of a variety of dimensions are excavated in snags and logs by larvae of wood boring beetles and the vacated galleries are often used by a variety of other insects. A native bee, the orchard mason bee (*Osmia* spp.), uses holes approximately 8 mm by several centimeters deep for egg laying. Artificial cavities for this beneficial bee can be created with a standard drill bit. A portion of the tree facing south should be selected to optimize temperature regimes needed by this bee. Holes should be about 8 cm (3 inches) deep with an 8 mm (5/16-inch) drill bit. The hole should be cleaned out so that rough edges do not impede the bees.

Honey bees (*Apis* spp.) were originally imported from Europe, but have become well established in the U.S. and have become essential pollinators for orchards, cranberries, and native plants. They commonly use hollow logs, decayed or hollow trees, and various other cavities for their nests. Bee nests are a delicacy for forest omnivores such as bears. Creation of cavities in trees, logs, and stumps can enhance the habitat for these bees. Suitable cavities can be excavated in erect trees and then covered with face-plates, that include small entrance holes, over the cavity. A tree should be selected in an open stand that receives plenty of sunlight. With a chainsaw, a cavity should be excavated approximately 1 cubic foot. A faceplate should be secured onto the cavity with a 1 centimeter entrance hole at the base or one long slit 1 centimeter in width. Hollow logs or trees with no entrance can be opened up to the exterior with a small drill to provide access. In addition to honey bees, wasps also commonly use these structures and contribute to both pollination and pest control.

Lady bugs (*Hippodamia* spp.) are predaceous insects that overwinter in tiny crevices in wood, logs, or stumps in areas with adequate insolation. Suitable size crevices can be constructed with a chainsaw in trees and stumps in sunny sites. The tip of the chainsaw should run approximately 15 cm beyond the bark layer in several locations of a snag and/or stump.

Discussion and Conclusion

Management activities will, incidentally, contribute to varying levels of habitat loss. Losses will vary, but in nearly all cases, rehabilitation can lead to enhancement of wildlife components faster than if habitats are unmanaged.

The first step to rehabilitation is to assess the damage of the activity with respect to wildlife habitat. It is important to evaluate the condition of vertical and horizontal elements of the habitat. If necessary, for example, cut green trees or partially decayed logs can be delivered from off-site to act as nutrition logs and habitat for wildlife. Logs should be selected so that they will reach mid-succession in the decay sequence when the regenerated forest stand can begin recruiting its own snags and downed logs. As a precaution, any downed logs brought into the rehabilitation area should be recruited as close as possible from the managed site and inspected to minimize the introduction of unwanted fungal diseases and insects.

Taking remedial action over the entire area of interest may not be feasible, however, and it is essential that remediation result in creation of a mosaic of habitats at a variety of scales that will provide habitat for prey, as well as perching, nesting, and denning sites for predators. If small mammals and birds are provided suitable cover and rest sites, they may cache seeds harvested in the surrounding green areas. Their feces will also inoculate the soil with fungal spores, some of which are essential to functioning forest, including mycorrhizal fungi.

Intensely burned areas may leave significant amounts of downed woody debris and standing snags. However, the habitat and nutrient benefits of these snags and debris may be severely limited if fire has caused the exterior of the wood to be case hardened. Case hardening results from moisture loss coupled with chemical changes that occur on the fire-exposed surface of wood. Case hardening increases the compressional strength and brittleness of the snag or log, and more importantly, seals off the nutritional resources within the tree. This sealing, along with the direct loss of bark and cambial nutrients, limits the usefulness of the post-fire dead wood for many species. Birds, mammals, and bark beetles cannot penetrate and shape case-hardened wood in their usual manner. Furthermore, reduction in vertical cover and loss of organic duff on the ground reduces the habitat suitability for numerous forest organisms.

The degree of success of artificial structures is generally proportional to on-site supervision by an experienced professional during enhancement activities. Without proper training and preparation, application of these methods could place workers in hazardous situations. Because the chainsaw is the tool of choice for many of the projects, it is strongly advised that workers be properly trained and certified to handle such equipment on the ground, and especially, when working above the ground in trees.

In the last three decades in which many of these techniques have been applied, it is apparent that there is an information gap in reporting either the success or failure of the techniques. Forest land managers and natural resource biologists should ensure that existing and future projects are monitored vigorously with the intention of documenting enhancement results or lack thereof. Wildlife habitat enhancement methods and techniques can be blended to retain and enhance not only threatened, endangered, and sensitive species, but also to include the total biotic composition that is associated with wood habitat. Some general observations have shed light on the suitability of the various restoration techniques presented in this paper and allow optimism for the success of many projects. Preservation and management of wildlife structures and associated biota that use them, and the workers performing their tasks in wood habitat retention areas, can be simultaneously achieved with foresight and innovative planning.

Acknowledgments

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Perspectives and Approaches to Management

An Ecological Functional Basis for Managing Wood Decay Elements for Wildlife[1]

Bruce G. Marcot[2]

Abstract

The traditional approach to managing decaying wood for wildlife has been to list species associated with snags, down wood, and other wood decay elements, and then to provide the kinds, sizes, and amounts of wood decay elements presumed necessary to meet their needs. An expanded approach more consistent with the spirit of ecosystem management would also describe those species' key ecological functions (KEFs). KEFs influence the ecosystem through trophic relations, species interactions, soil aeration, primary cavity and burrow excavation, and dispersal of fungi, lichens, seeds, fruits, plants, and invertebrates. These "functional webs" can be described for wildlife species associated with various wood decay elements (snags, down wood, litter, duff, mistletoe brooms, dead parts of live trees, hollow living trees, natural tree cavities, bark crevices, and live remnant or legacy trees) in Washington and Oregon. Information on species' KEFs also is part of the DecAID wood decay management advisory model. The challenge is posed for management to think functionally beyond simple species-habitat relations, as to the broader role of wood decay in supporting functional webs.

Introduction

Current approaches to managing wood decay elements for wildlife generally focus on identifying the wildlife species associated with such elements and the amount and distribution of such elements (mainly snags and down wood) deemed necessary to support those species. Appropriate silvicultural or vegetation management guidelines are then crafted to provide the snag and down wood levels.

However, this is but one side of the ecological equation. It may be useful to also recognize and manage for the key ecological functions (KEFs) of wildlife because they, in turn, influence environmental elements and ecosystem processes affecting other species. The term "key ecological functions" refers to the major ecological roles of organisms in their ecosystems, as differentiated from abiotic ecosystem processes such as fire and disturbance events. A classification of KEFs has been proposed elsewhere (Marcot and others 1997, Morrison and others 1998). In a database, each wildlife species can be coded as to its KEFs as well as the

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macrohabitats and habitat elements it uses. By using this approach, the manager can identify the macrohabitats and habitat elements present in an area, the species associated with those habitats, and the array of KEFs associated with those species. In this way, the manager can begin to explicitly consider the ecological functions of wildlife in a repeatable and rigorous fashion.

This paper demonstrates how the KEFs of terrestrial vertebrate wildlife species associated with decay wood elements in Oregon and Washington can be considered in forest management. I draw from species-habitat and species-KEF databases developed for the Oregon-Washington Species Habitat Project (SHP) (Johnson and O'Neil 2001; Marcot and Vander Heyden 2001) and for the Interior Columbia Basin Ecosystem Management Project (ICBEMP) (Marcot and others 1997). I use the term "manager" to refer to both natural resource decision-makers and at least some of the specialists who support them.

Methods

Developing the Species-environment Relations Databases

The species-habitat and KEF databases I used from SHP and ICBEMP were developed from literature surveys and expert peer reviews. The SHP project developed databases for terrestrial and marine non-fish vertebrates of Washington and Oregon, whereas ICBEMP developed databases for species groups and rare species of lichens, bryophytes, vascular plants, soil microorganisms, and terrestrial invertebrates, and for all species of non-fish vertebrates, in the interior Columbia River Basin and portions of the northern Klamath and Great Basins in the U.S.

In SHP and ICBEMP, species' environmental correlates included snags, down wood, and other wood decay substrates. The SHP database used the classification system listed by Neitro and others (1985) to denote five decay classes of snags: 1 = hard and mostly intact, 2 = hard with some loss of small branches, 3 = moderately decayed with more extensive loss of small branches and some sloughing bark, 4 = decayed with extensive branch and bark loss, and 5 = advanced decay typically with loss of most branches and bark.

KEFs included a wide range of categories of ecological roles of organisms. I arranged environmental correlates and KEFs into hierarchical classifications to determine which and how many species pertain to general and specific habitat elements and ecological roles. The major categories of environmental correlates in the classification include sundry biotic and abiotic substrates as well as influences from other organisms. The major categories of KEFs include trophic, nutrient, organismal, disease, soil, wood, water, and vegetation relations. In the databases, environmental correlates and KEFs are mostly represented categorically and should be viewed as working hypotheses of species' environmental and ecological relations.

The specific categories of environmental correlates and KEFs pertinent to wood decay elements are listed in *table 1.* I queried the databases to determine which individual wildlife species and species groups have snags, down wood, and other wood decay elements as part of their environmental correlates and ecological functional roles. I summarized database queries across species taxonomic classes and arrayed the KEFs as functional webs (Marcot and Vander Heyden 2001). Functional webs display the array of ecological roles and environmental correlates pertaining to species associated with wood decay elements.

Table 1—*Categories of key environmental correlates (habitat elements) and key ecological functions of wildlife species related to wood decay elements, from the Oregon-Washington Species Habitat Project (Johnson and O'Neil 2001). Category numbers refer to the classification systems developed for the species databases. (Similar categories were first developed for the Species-Environment Relations database for the Interior Columbia Basin Ecosystem Management Project; Marcot and others 1997.)*

Key Environmental Correlates (Habitat Elements):	
Forest/woodland elements:	
Down wood:	
1.1.1	down wood (includes downed logs, branches, and root wads, in any context)
1.1.1.1	decay class
1.1.1.1.1	hard [class 1, 2]
1.1.1.1.2	moderate [class 3]
1.1.1.1.3	soft [class 4, 5]
1.1.1.2	down wood in riparian areas
1.1.1.3	down wood in upland areas
1.1.2	litter
1.1.3	duff
Snags:	
1.1.14.1	snags
1.1.14.1.1	decay class
1.1.14.1.1.1	hard [class 1,2]
1.1.14.1.1.2	moderate [class 3]
1.1.14.1.1.3	soft [class 4,5]
1.1.14.2	snag size (dbh)
1.1.14.2.1	seedling <1" dbh
1.1.14.2.2	sapling/pole 1-9" dbh
1.1.14.2.3	small tree 10-14" dbh
1.1.14.2.4	medium tree 15-19" dbh
1.1.14.2.5	large tree 20-29" dbh
1.1.14.2.6	giant tree ≥30" dbh
Other wood decay elements:	
1.1.14.4	mistletoe brooms/witches brooms
1.1.14.5	dead parts of live tree
1.1.14.6	hollow living trees (chimney trees)
1.1.14.7	tree cavities
1.1.14.8	bark (includes crevices/fissures, loose or exfoliating bark)
1.1.14.9	live remnant/legacy trees
Shrubland/grassland elements:	
Snags:	
1.2.12.1	snags
1.2.12.1.1	decay class
1.2.12.1.1.1	hard
1.2.12.1.1.2	moderate
1.2.12.1.1.3	soft

(*table 1* continued)	
Snags (continued):	
1.2.12.2	snag size (dbh)
1.2.12.2.1	shrub/seedling <1" dbh
1.2.12.2.2	sapling/pole 1-9" dbh
1.2.12.2.3	small tree 10-14" dbh
1.2.12.2.4	medium tree 15-19" dbh
1.2.12.2.5	large tree 20-29" dbh
1.2.12.2.6	giant tree ≥30" dbh
Key Ecological Functions:	
Down wood:	
6.1	physically fragments down wood
Snags:	
3.9	primary cavity excavator in snags or live trees
3.10	secondary cavity user
6.2	physically fragments standing wood
8.1	creates standing dead trees (snags)

Clustering Wood Decay Elements by Species Usage

I developed a table listing each vertebrate wildlife species' use of eight wood decay elements: snags, remnant, or legacy trees (which may have dead parts), mistletoe and witch's brooms, dead parts of live trees, hollow living trees, tree cavities, bark crevices, and down wood (coarse woody debris). I depicted use as a binary function: 1 if a species was associated, 0 if not. I then calculated binary similarity coefficients among the wood decay elements based on species' use, and a hierarchical cluster classification using single linkage (nearest neighbor) and Euclidean distances among clusters. Results describe the similarity of wood decay elements according to usage by wildlife species.

Depicting the Functional Web

I queried the SHP database to determine the KEFs associated with species tied to wood decay elements. I also queried the ICBEMP database to determine the KEFs of invertebrates associated with wood decay elements. Results depict the kinds, breadth, and redundancy of ecological functions of both vertebrate wildlife species and invertebrate species associated with wood decay. This information is also part of the DecAID wood decay management advisory model (Mellen and others 2002).

Results and Discussion—Environmental Relations And Functional Roles Of Species Associated With Wood Decay Elements

Relations of Wildlife and Wood Decay Elements

In this section I describe patterns of terrestrial vertebrate wildlife species in Washington and Oregon that are related to wood decay elements. This assessment helps determine which sets of species may be uniquely provided by the various wood decay elements.

Standing Tree Elements

In Washington and Oregon, a total of 96 wildlife species are associated with snags in forest (93 species) or grassland/shrubland (47 species) environments. In forest environments, these include 4 amphibian, 63 bird, and 26 mammal species *(fig. 1).* In addition, 51 wildlife species are associated with tree cavities, 45 with dead parts of live trees, 33 with remnant or legacy trees (which may have dead parts), 28 with hollow living trees, 21 with bark crevices, and 18 with trees having mistletoe or witch's brooms.

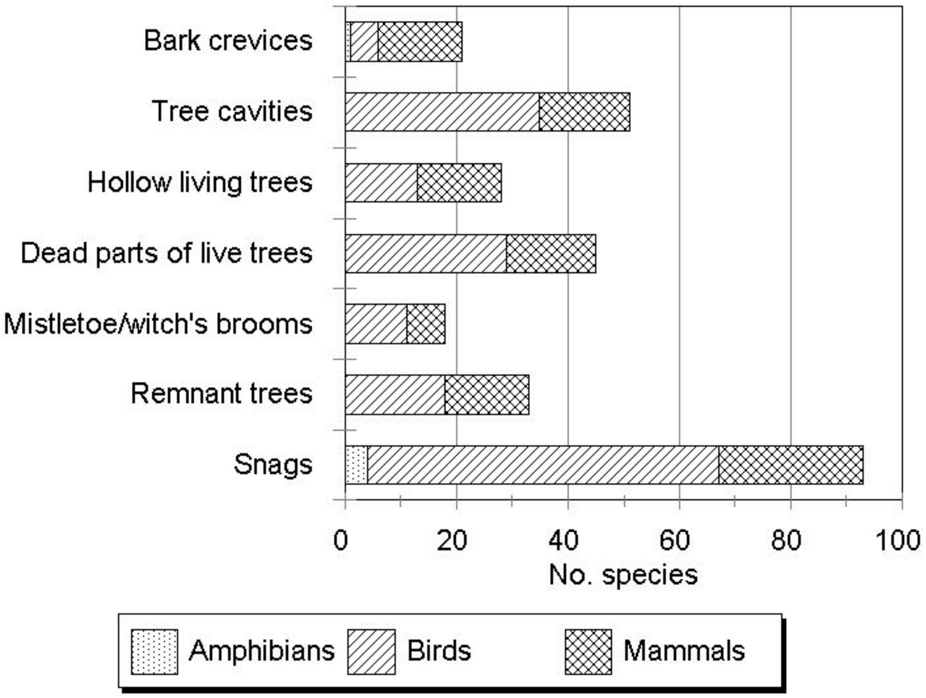

Figure 1—Number of wildlife species associated with standing wood decay elements in forest habitats of Washington and Oregon. (Data are from the Oregon-Washington Species Habitat Project [Johnson and O'Neil 2001]).

Of the 93 wildlife species associated with snags in forest environments, 21 are associated with hard snags (snag decay classes 1 and 2), 20 with moderately decayed snags (snag decay class 3), and 6 with soft snags (snag decay classes 4 and 5) *(fig. 2).* Five of the 21 species are associated only with hard snags: great blue heron *(Ardea herodias),* hooded merganser *(Lophodytes cucullatus),* pileated woodpecker *(Dryocopus pileatus),* pygmy nuthatch *(Sitta pygmaea),* and wood duck *(Aix sponsa).* Three of the 20 species are associated only with moderately decayed snags: northern flying squirrel *(Glaucomys sabrinus),* ruffed grouse *(Bonasa umbellus),* and white-headed woodpecker *(Picoides albolarvatus)* (although white-headed woodpecker might not associate only with moderately decayed snags in eastside pine forests [Laudenslayer, pers. comm.]). Only chestnut-backed chickadee *(Parus rufescens)* was associated solely with soft snags. The remainder of the 93 species use two or more snag decay groups. According to the SHP database, most snag-using wildlife species are associated with snags > 36 cm diameter at breast height (dbh), and about a third of these species use snags > 74 cm dbh *(fig. 3;* Marcot and others 2002).

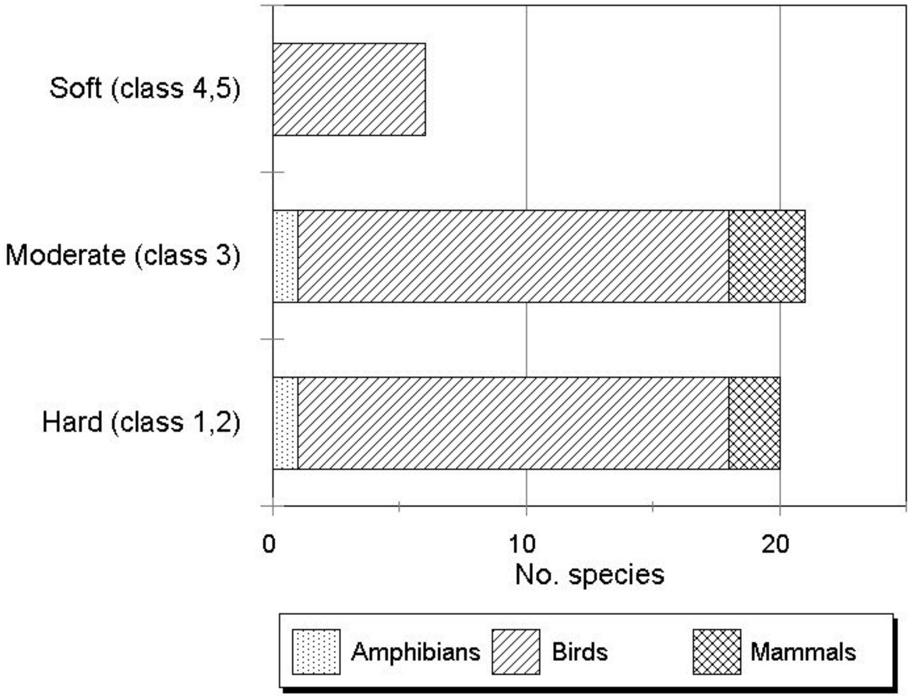

Figure 2—Number of wildlife species associated with three decay stages of snags in forest habitats of Washington and Oregon. (Data are from the Oregon-Washington Species Habitat Project [Johnson and O'Neil 2001]).

Down Wood Elements

In forest environments, 74 wildlife species are associated with down wood (coarse woody debris), 28 with litter (undecomposed fine woody debris), and 11 with duff (decomposed woody debris and other vegetation matter underlying the litter layer) *(fig. 4).* Of these species, 58 are associated exclusively with down wood, 10 exclusively with litter, and none exclusively with duff.

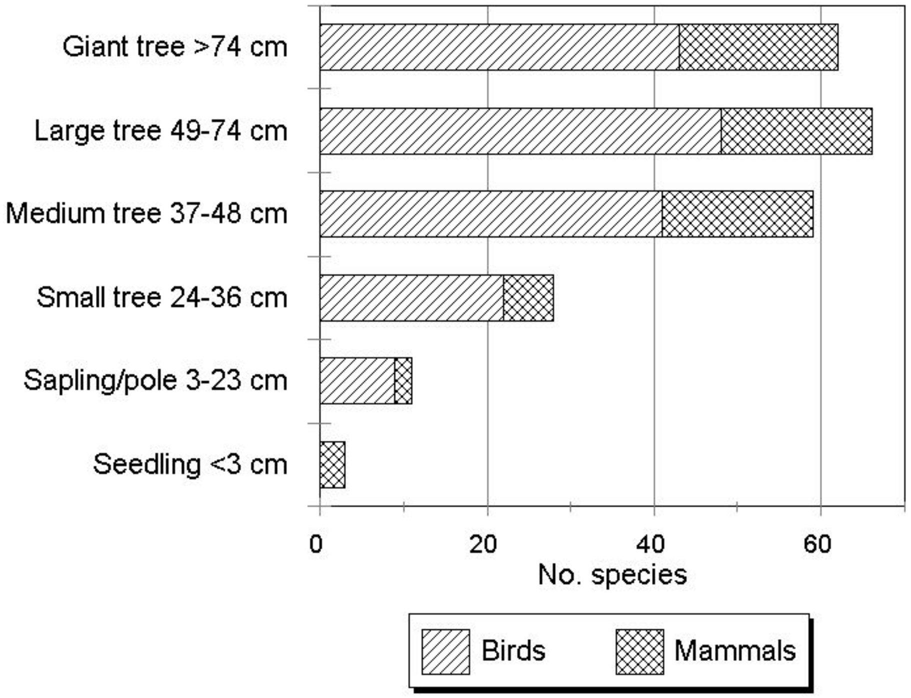

Figure 3—Number of wildlife species associated with size classes (dbh or diameter at breast height) of snags in forest habitats of Washington and Oregon. (Data from the Oregon-Washington Species Habitat Project [Johnson and O'Neil 2001]).

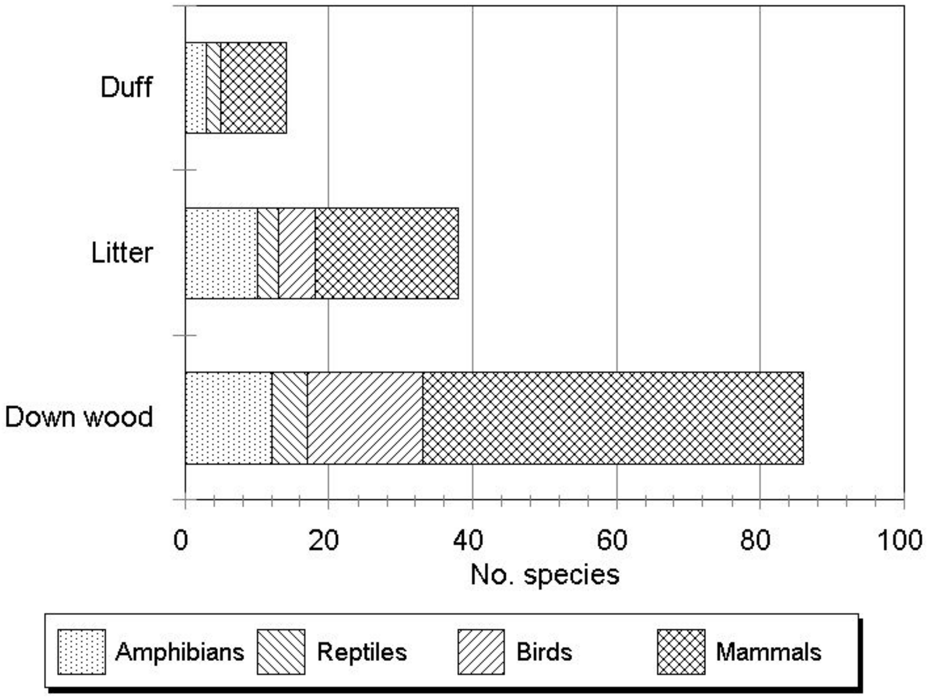

Figure 4—Number of wildlife species associated with terrestrial wood decay elements in forest habitats of Washington and Oregon. (Data from the Oregon-Washington Species Habitat Project [Johnson and O'Neil 2001]).

Similarity in Wood Decay Use

As may be expected, different species tend be associated with snags and down wood. Of 184 wildlife species associated with either snags or down wood, only 30 use both, 86 use down wood and not snags, and 128 use snags and not down wood.

Similar trends appear when considering the fuller array of species associated with other wood decay elements. Results of clustering wood decay elements by species usage *(fig. 5)* suggest that the most unique sets of wildlife species (at least 50 percent dissimilar in species associations) are those that use mistletoe or bark crevices. Intermediate in similarity are the sets of wildlife species using live hollow trees, live remnant or legacy trees, and down wood. The most similar are the sets of wildlife species that use tree cavities, snags, and dead parts of live trees, although there are still substantial differences in the species associated with each of these three elements. This analysis suggests that no one wood decay element provides for all wildlife species associated with wood decay.

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                                                           Distances
           0.0                                                                                                     1.000
MISTLETOE        -----------------------------------------------------------\
                                                                            |----------------------------------------------
DN_WOOD          -----------------------------------------------\           |
                                                                +\          |
TREE_CAV         -----------------------------------\           ||          |
                                                    +\          ||          |
SNAGS            -----------------------------------/|          ||          |
                                                     +----------+|          |
DEAD_PRT         ------------------------------------/          ||          |
                                                                ||          |
LIVE_REMN        -----------------------------------------------/|          |
                                                                 +---\      |
HOLLOW           ------------------------------------------------/   |      |
                                                                     +------/
BARK_CREV        ----------------------------------------------------/
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Figure 5—Hierarchical cluster classification of wood decay elements by wildlife species association in forest habitats of Washington and Oregon. Wood decay elements with greater similarity of species usage have shorter between-cluster distances than do elements with greater dissimilarity. Data on the 162 species used in this analysis were binary (associated or not with each element), and clustering was done using single linkage (nearest neighbor) with Euclidean distances based on a binary correlation matrix. (Data are from the Oregon-Washington Species Habitat Project [Johnson and O'Neil 2001]).

Functional Roles of Vertebrate Wildlife Species Associated with Wood Decay Elements

Results presented so far pertain to the traditional approach to depicting wildlife-habitat relations. Taking a more functional view adds a new dimension to this approach by depicting the varieties of KEFs, beyond those pertaining just to wood decay, performed by wildlife species that are associated with wood decay elements (Machmer and Steeger 1995). Such ecological roles comprise a surprisingly broad array of functional categories, spanning many trophic and dietary relations, dispersal roles, and organismal, soil, wood, water, and vegetation relations.

As an example, I will focus on the functional web of wildlife species in Washington and Oregon associated with down wood in forest environments *(fig. 6),* as depicted in the SHP databases. This set includes 86 species of heterotrophs and 59 species that serve as prey for other species. Of the heterotrophs, 57 percent are primary consumers, 77 percent are secondary consumers, and others (each < 10 percent) comprise tertiary consumers, carrion feeders, cannibals, and coprophages (percentages may sum > 100 because some species play multiple roles). Of the 49 primary consumer species associated with down wood, 53 percent are spermivores (seed-eaters), 43 percent are fungivores (fungi-eaters), 29 percent are grazers, 27 percent are frugivores (fruit-eaters), and the rest (each < 20 percent) comprise 10 other primary consumption categories. Of the 66 secondary consumer species associated with down wood, 88 percent are insectivores (consume insects and other invertebrates), 33 percent are vertebrate predators, 20 percent are ovivores (egg-eaters), and 6 percent are piscivores (fish-eaters). It may come as a surprise to some managers that down wood provides habitat, at least in part, for so wide an array of species with such a broad set of trophic and dietary functions.

Organismal relations of wildlife associated with down wood include a number of symbiotic and other interspecific interactions beyond those related to dietary and trophic habits. Of the 86 wildlife species associated with down wood, 38 percent serve as dispersal agents, transporting plants or animals. Of this set, 29 species disperse seeds and fruits, 10 disperse fungi, 7 disperse lichens, 1 disperses plants, and 1 disperses invertebrates.

Other organismal relations supported by down wood include potential control of insect or vertebrate populations, pollination, creation of feeding or nesting opportunities for other species, and serving as hosts for nest parasites.

Some organismal relations are symbiotic functions. For example, seven wildlife species associated with down wood create feeding or nesting structures that are in turn used by other species. Four wildlife species associated with down wood are also primary cavity excavators and 13 are secondary cavity users. Twenty-six wildlife species associated with down wood are primary burrow excavators, and another 29 species are secondary burrow-users. Fourteen wildlife species associated with down wood are primary creators of terrestrial runways and paths, and another 29 species are secondary users of runways and paths created by other species.

Twenty-three wildlife species associated with down wood can potentially improve soil structure and aeration by burrowing and digging. This, in turn, could help maintain or improve soil conditions for plants and other animals.

Through digging, gnawing, and probing, mostly for foraging, two wildlife species associated with down wood serve to fragment standing wood, seven fragment down wood, and 2 kill trees and create snags. This could have positive feedback ramifications for providing for species associated with wood decay elements and for initiating the incorporation of organic matter into soils.

Two ungulate species associated with down wood can create small ponds and wetlands by wallowing. There are seven mammal species associated with down wood that browse on trees or shrubs, and four mammal species that graze on grasses or forbs, that can alter vegetation composition, structure, cover, and seral conditions for other species.

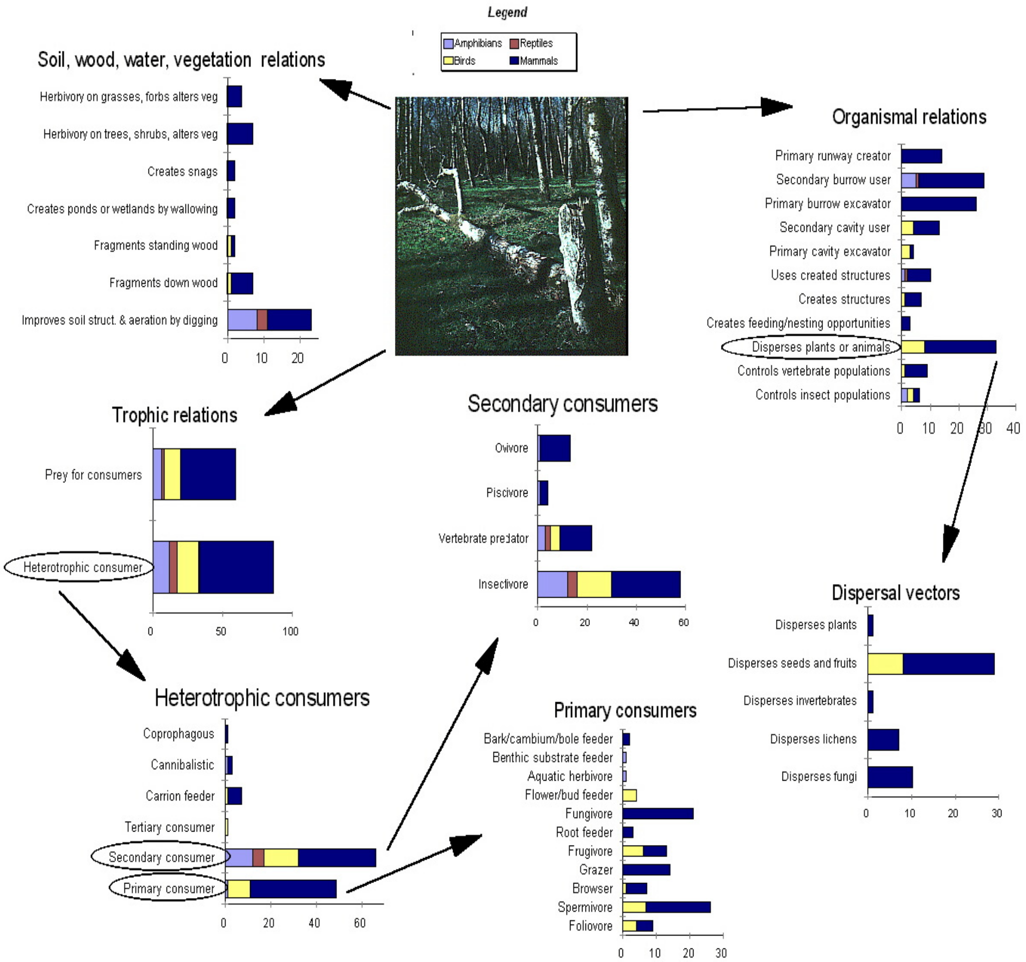

Figure 6—The ecological "functional web" of down wood, showing the number of associated wildlife species and their key ecological functions (ecological roles they play) in forest habitats of Washington and Oregon. (Data are from the Oregon-Washington Species Habitat Project [Johnson and O'Neil 2001]).

In summary, down wood can be viewed as the center of a "functional web" of ecological roles. As such, down wood, or any of the wood decay elements, provides at least some of the habitats used by many wildlife species that in turn can influence their environment and other species in diverse and unexpected ways. Further, functional webs can be described for each of the wood decay elements *(figs. 1-4),* and the webs differ slightly or greatly among the elements. For example, there tends to be a lesser percentage of primary consumer wildlife species associated with snags (40 percent of all heterotrophs associated with snags) than with down wood (57 percent of all heterotrophs associated with down wood), and a greater percentage of secondary consumers associated with snags (95 percent) than with down wood (77 percent). Grazers and foliovores comprise a greater percentage of primary consumers associated with down wood (29 percent and 18 percent of all down wood-associated primary consumers, respectively) than with snags (8 percent and 11 percent, respectively). These differences suggest that no single wood decay element provides for all functional groups of wildlife and that different wood decay elements play complementary roles in providing for all functions collectively.

Functional Roles of Invertebrate Species Associated with Wood Decay Elements

The ICBEMP database includes selected individual species and functional groups of invertebrates. In general, invertebrates play key ecological roles, in forest ecosystems of the western U.S., pertaining to wood decay functions (Schowalter and others 1997). Their ecological roles are poorly studied and no complete functional web can be described for them. However, a few examples can be provided.

Invertebrates associated with down wood in the interior Columbia Basin span a range of KEF categories and ecological roles. Here are some examples. As an associate of down wood, the checkered beetle *Enoclerus sphegeus* (Coleoptera: Cleridae) is an important predator of bark beetles (Coleoptera: Scolytidae) and other subcortical beetles and provides a trophic link in the exo- and sub-cortical microhabitats in snags and coarse woody debris. A number of wood-boring and—chewing insects associated with down wood, including the carpenter ant *Camponotus modoc*, greatly aid wood fragmentation and decomposition.

Several invertebrates associated with down wood collaborate in pollination and production of native fruits and seeds used as food by mammals, birds, ants, and other frugivorous or spermivorous insects. Examples include a number of bee species (Hymenoptera), such as small carpenter bees (*Ceratina acantha*, Anthophoridae), plasterer bees (*Hylaeus lunicraterius*, Colletidae), and several species of leafcutting bees (*Ashmeadiella sculleni, Hoplitis fulgida, Hoplitis productua subgracilis, Osmia bruneri, Osmia cascadica, Proteriades orthognathus*, and others; Megachilidae). Even more bee species (especially of family Megachilidae) performing this function are associated with snags.

The gossamer-winged butterfly (*Mitowra johnsoni*; Lycaenidae: Lepidoptera) is an example of an invertebrate associated with mistletoe brooms. In its larval form, this species is a defoliating herbivore, but it also serves as food for birds, small mammals, and predaceous invertebrates.

Even bark beetle species such as *Scolytus ventralis* (Scolytidae: Coleoptera) have useful ecological functions. By killing trees, this species and its kin may increase likelihoods of stand-replacing fires by increasing standing and down woody debris. In some management plans, this is not a desirable outcome. However, this ecological function has secondary beneficial effects of promoting nutrient cycling, and altering tree density, canopy structure, age distribution, and species composition of stands. This provides habitat for a wide variety of plants and animals. Bark beetles of many species also serve as prey for woodpeckers and other vertebrate species (Otvos 1965).

In summary, invertebrates associated with wood decay elements play multiple ecological roles in forest ecosystems, many of them beneficial to other plant and animal species.

Management Implications for Structures and Functions

Considering Ecological Functions in Ecosystem Management

It is well known that many land and resource management activities change the type, amount, and distribution of wood decay elements. Less well known are the ramifications of those changes on the functioning of ecosystems.

The SHP databases include a table listing wildlife habitat elements that can be directly affected by management activities. The database includes 152 categories of management activities listed under 13 general headings of types of land use such as fire management, riparian and aquatic resource management, road management, agriculture, mining, forest management, and others (Vander Heyden and Marcot 2001). The database indicates that the wood decay elements *(figs. 1, 4)* are potentially influenced by 44 types of management activities across 9 general headings of land use. Clearly, the potential influence of management on wood decay elements for wildlife is not trivial.

If resource management is to provide for "fully functional" ecosystems—one of the possible goals of ecosystem management (e.g., Goldstein 1999)—then the approach offered in this paper provides one way of determining the degree to which an ecosystem is fully functional. The manager can specify land management activities under consideration and then determine which habitat elements and associated species could be influenced by the activities (positively or negatively). Then, the manager can determine the set of KEF categories associated with the affected species and compare this with other alternative management activities or expected changes in wildlife habitats, structures, and elements over time.

What patterns should the manager look for? A listing of species- and community-patterns of ecological functions was offered by Marcot and Vander Heyden (2001). One functional pattern that can be easily determined by querying the databases discussed includes that of functional redundancy or the number of different wildlife species with the same KEF. As functional redundancy declines, the degree to which the community can resist or be resilient to perturbations may also decline (MacNally 1995, Naeem 1998). Other functional patterns of potential interest to ecosystem managers may include calculating functional richness and total functional diversity, describing functional webs and functional profiles, mapping functional hot and cold spots, identifying functional keystone and critical link species, and identifying other patterns and examples (Marcot and Vander Heyden 2001).

I interpret the results as testable working hypotheses of ecological roles and relations, and I challenge resource managers to think broadly about the functional roles of organisms associated with wood decay elements as a facet of ecosystem management. Overall, it is my assumption that degrading the functional matrix of a community serves to decrease its resilience, stability, natural diversity, and even sustainable productivity for desired conditions and products. The manager can determine the risk of such degradation by evaluating how a specific set of proposed activities can affect functional patterns associated with wood decay elements.

The manager might also assess KEFs of wildlife in the context of the capability of the land to produce wood decay elements. Forest and woodland stands differ in their capacity to produce dead wood elements. Such capacity typically changes over time as well, and is related to site condition and history, stand structure, occurrence of abiotic disturbances such as fire and wind, and other site and landscape factors, as well as to some of the ecological roles of organisms, as discussed above, that can serve to create or alter wood decay elements. Managing to maintain functional roles and groups of organisms, by managing for habitats and environmental conditions providing for organisms with desired ecological roles (KEF categories), should account for site and landscape conditions that also affect the distribution and abundance of wood decay and other habitat elements.

The analysis showed that no one wood decay element provides for all wildlife species associated with wood decay. In fact, it seems that all wood decay elements included in this analysis may be necessary to provide for all associated wildlife species. Thus, the manager might attend to the fate of all such elements, at least to help determine which associated species and functions would be provided. Because many of the elements of wood decay are not necessarily represented by snags per se, the manager may wish to explicitly include them along with snags in stand inventories and in management plans. At the least, managers could determine the influence of forest management actions on such elements and on the wildlife and their ecological functions associated with them.

Validation

Plainly, much empirical research remains to be done to verify and quantify the ecological functions of wildlife species, including those associated with wood decay elements and especially invertebrates. I have not discussed such functional roles of fungi, lichens, bryophytes, vascular plants, and microorganisms, but those associated with wood decay elements play many key roles in ecosystems and most need sound study.

Also needing further explication and study is that of quantity: how much functionality is enough? How much would match historic, or reference, landscapes and desired stand conditions? There is scant research available on the rates of ecological roles, such as nutrient redistribution by snag-using bats, or control of populations of micorhizzal fungivorous springtails by predatory spiders associated with down wood as can affect commercial tree production.

A related information need is how to distribute wood decay elements in space and time to provide for ecological functions of desired associated organisms. Work in progress (Marcot and others, in preparation) and recent inventory analyses (Ohmann and Waddell 2002) suggest that management standards for numbers of snags and down wood in forests of the Pacific Northwest have been far too low as compared with unharvested reference conditions, and that densities and local distributions (such as clumping) of snags and down wood vary considerably within and among stands and according to a variety of local disturbance factors.

I expect that many of the ecological functional relations described in this chapter, even for relatively well-known vertebrate wildlife species, will change in kind or degree with empirical study. My intent here is to provide a framework from which such functions can be repeatably described as working management hypotheses, and then tested through experimental studies in the field. Ultimately, the aim is to validate the degree to which land and resource management activities serve to support, restore, or compromise the functional vitality of natural communities and the sustainable production of resources.

Conclusions

I challenge land and resource managers to think functionally when prescribing activities that influence snags, down wood, hollow trees, and other wood decay elements. It is time to move beyond simply identifying which wildlife species (plants and animals) are associated with wood decay elements. The approach offered here can provide a practical method of establishing standards and guidelines for managing attributes that have ecological value but in the past have been ignored or deliberately selected against.

Describing the direct ecological roles of wood decay, including soil stabilization, organic matter input to soils, nutrient cycling, provision of microhabitats for plants and animals, and other direct ecological benefits (e.g., Means and others 1992, O'Connor and Harr 1990), is an important step toward a more functional approach to wood decay management. However, a next major step is to describe the fuller functional web of the ecological roles of wildlife species that are in turn associated with wood decay elements. From this approach, the manager can determine the degree to which their management actions will provide for fully functional ecosystems, and how management activities influencing wood decay components can affect that functionality.

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A Case Study of Habitat Conservation Plans and the Protection of Snags and Coarse Woody Debris on Industrial Forest Lands[1]

Lorin L. Hicks[2] and Henning C. Stabins[2]

Abstract

Forest practices on private industrial timberlands have steadily progressed to incorporate many of the issues and approaches currently in use on public forests. One of the most significant advances for protecting wildlife habitat on private lands has been the development of Habitat Conservation Plans (HCP). Originally developed as a planning process for landowners to mitigate for the incidental status of threatened and endangered species, HCPs have expanded to become long-term, multi-species landscape plans designed to address many aspects of wildlife and fish management. Plum Creek completed a 50-year HCP for 64,751 hectares of company land in Washington's central Cascades Mountains in June 1996. The HCP addresses the biological needs of all vertebrate species, including anadromous fish and cavity-dependent wildlife.

Introduction

The recognition of snags and coarse woody debris as important wildlife habitat elements and their retention on the landscape has been one of the most dramatic changes to commercial forest practices in recent years. Similarly, Habitat Conservation Planning as authorized under the Endangered Species Act has recently provided the opportunity for industrial landowners to develop innovative land management plans with the federal government. These plans provide not only substantive habitat protections for fish and wildlife resources but also regulatory predictability for private landowners. This paper discusses the development and implementation of Plum Creek's Cascades Interstate-90 (I-90) Habitat Conservation Plan (HCP; Anonymous 1996a), with particular emphasis on how the plan addresses habitat needs for wildlife associated with snags and coarse woody debris.

Landowner Considerations

The content and configuration of landowners' properties is an important determinant to landscape planning. A major portion of Plum Creek's ownership in the Cascades Mountains of Washington is in the I-90 corridor near Snoqualmie Pass,

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96 kilometers east of Seattle. The region supports many important resources and potentially conflicting land uses, such as roadless and motorized recreation, agriculture, water storage, highways, powerline and railroad routes, ski areas, communities, and recreational development. The intense and growing public use of this area places commercial forestry in a highly visible operating arena.

Another feature of Plum Creek's property in the region is the "checkerboard" pattern of intermingled ownership with the USDA Forest Service. This ownership pattern stems from the railroad land grants of the late 1800s and presents a challenge for both public and private land managers. Despite the completion of land exchanges to resolve this dilemma, the pattern continues to exist in many areas and requires landowners to coordinate and communicate closely on protection of public resources.

Lessons Learned from Past Management

Over the past 20 years, a major paradigm shift has occurred in commercial forest management. Driving this paradigm shift is the realization that forest practices intended to protect wildlife and fish habitat were actually having the opposite effect. For instance, dispersing clearcuts was thought to be good for habitat diversity but now increases the risk of forest fragmentation. Mandatory stream cleanout to remove logging debris was considered prudent to avoid debris dams; however, we now know that this practice removed the large wood essential for bank stability and fish habitat. Finally, increased use of dead and defective trees and removal of "danger trees" was considered efficient years ago but has been shown to contribute to reduction in habitat for cavity-dependent wildlife.

The listing of the northern spotted owl *(Strix occidentalis)* in 1990 created yet another force for changing paradigms on private lands. Experiments with "New Forestry" concepts of retaining structural components from older forests laid the groundwork for this paradigm on Plum Creek lands (Hicks 1991, Kohm and Franklin 1997). Silvicultural experiments to extract high-value timber while retaining functional spotted owl habitat confirmed that spotted owls could use post-harvest stands that normally would have been clearcut and regenerated under conventional practices.[3] Moreover, silvicultural alternatives that focused on retention of down logs, standing snags, and residual large green trees provided habitat for a wide variety of wildlife species (Stofel 1993).

The need for a new paradigm was both biological and economic. Federal and state regulations (Anonymous 1991, 1992, 2000) to address spotted owl habitat required the designation of 2.9 kilometer radius circles around spotted owl nest sites and the retention of 40 percent (approximately 1,052 hectares) of the area within the circle as owl habitat. In 1994, Plum Creek had 107 owl protection circles affecting its ownership in the I-90 corridor.

Incentives for Habitat Conservation Planning

The voluntary Habitat Conservation Planning process, added to the Endangered Species Act (ESA) in 1982, was little understood and seldom used by private landowners until recently (Anonymous 1995). Increased interest in HCPs stems in

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[3] Unpublished data on file, Plum Creek Timber Company, Seattle, Washington.

part from the desire to lessen the economic impact resulting from the ESA's prohibition and from the U.S. Department of Interior's policies offering regulatory incentives. These incentives, including pre-listing agreements, multi-species permits, the No Surprises policy, and Safe Harbor agreements, provide valuable regulatory certainty to the private landowner willing to commit the resources to complete an HCP (Anonymous 1996b).

For a private landowner like Plum Creek in the Pacific Northwest, the incentives to do an HCP include the following:

- Social—People's changing expectations for forestry.
- Scientific—Ecosystem management; assure sustained production of all forest resources.
- Political—Approval and implementation of the Northwest Forest Plan (Anonymous 1994) on Federal lands and checkerboard ownership patterns.
- Legislative—Endangered Species Act mandates the HCP process.
- Economic—Owl circles and associated costs.

Description of Plum Creek's Cascades HCP

Plum Creek's Cascades HCP currently covers seven listed species under the incidental take permit: spotted owl, marbled murrelet, grizzly bear, gray wolf, Canada lynx, steelhead salmon, and bull trout. The plan also identifies over 280 other unlisted vertebrate species in the Implementation Agreement. The planning period of 50 years can be extended to 100 years if certain conditions are met at the end of the first 50-year period. The plan was based on both a habitat and species-specific approach.

The HCP was developed as an ecosystem management plan designed to complement the Northwest Forest Plan for Federal lands. Approaches and strategies in the HCP are tiered to those in the Northwest Forest Plan, such as the protection of spotted owl sites near Late Successional Reserves and the extension of a riparian reserve network onto the company's lands.

The HCP is based on a forest stand classification system that describes forest conditions from stand initiation to old-growth. Conditions were mapped across all ownerships in the 169,162 hectare planning area. Two hundred and eighty-five species of animals known in the HCP area were grouped into guilds based on their life history requirements. These guilds, termed "Lifeforms," were then associated with one or more forest stand types of the classification system to identify their suitable breeding habitat. These forest stand structures and habitats are "grown" into the future using forest growth models that integrate differing harvest levels among State, Federal, and private landowners. At any point in the future, the amounts and locations of these forest stand types and habitats can be estimated.

Since riparian areas are important to many fish and wildlife species, a riparian management strategy was developed. These areas not only provide the necessary protection of elements important for in-stream habitat conditions, such as large woody debris, temperature moderation, nutrient input, and erosion control, but these areas also provide habitat and dispersal routes for upland species. A network of riparian habitat areas forms the core of the HCP's wildlife habitat protection strategy.

In addition, 38 mitigation measures were developed to provide species-specific protection or add to general wildlife and fisheries conservation. Examples of these mitigation measures include:

- Completing comprehensive watershed analyses for the majority of the planning area.
- Maintaining a minimum of 6 percent of the company's ownership as spotted owl nesting, roosting, and foraging habitat.
- Deferring from harvest 751 hectares of owl habitat for 20 years at key owl sites.
- Surveying 104 hectares of suitable marbled murrelet habitat.
- Employing a variety of management practices to provide secure grizzly bear habitat in the North Cascades Recovery Zone.
- Delaying operations near active spotted owl and northern goshawk nest sites until after the breeding season.
- Adjusting operations to reduce potential disturbance to gray wolves and their den sites.
- Maintaining forested wetlands and buffer zones surrounding cave entrances and talus slopes.

How Snag and Course Woody Debris Issues Were Addressed in the HCP

Mitigation measures in the HCP established desired density levels for defective trees, recruitment trees, and course woody debris (CWD) for post-harvest conditions (e.g., three wildlife reserve trees, three green recruitment trees, and two down logs for each acre harvested). Wildlife reserve trees are defined as defective or deformed live trees or dead snags that are observably sound, not hazardous to workers, and can be retained during the harvest (Anonymous 2000). Green recruitment trees are live trees that could serve as wildlife reserve trees in the future. The abundance and density of these structural elements are also measured in the forest stands representing structural classes to validate the wildlife-habitat associations made during modeling. Snag and CWD issues were also addressed indirectly during analysis of fuel loading and insect damage potential across the landscape through time. Forest health issues that were considered in the HCP development are also discussed.

Modification of Snag-dependent Wildlife Guilds and Modeling

The snag-dependent wildlife guilds, Lifeforms 13 and 14, were modified during the HCP peer review process. Lifeform 13 contains the primary cavity excavators, and Lifeform 14 contains the secondary cavity users. Species within these Lifeforms vary with regard to the size of snags required for life history needs. To better associate these species with the appropriate forest stand structures that could supply the necessary snag sizes, these Lifeforms were each separated into subgroups based on species' snag requirements. Lifeform 13 contains species such as hairy and downy woodpeckers and included some of the younger forest types (e.g., pole timber and dispersal forests) as part of their habitat associations. Lifeform 13a contains species such as pileated, white-headed, and Lewis's woodpecker (which have more stringent requirements for large diameter snags or defective trees) and are associated with mature and older forest structure stages for modeling and impact analyses. Lifeform 14 contains species such as chestnut-backed chickadees and red-breasted nuthatches. Lifeform 14a contains species such as the fisher and flammulated owl.

In addition to subdividing these guilds, we recognized that due to a change in forestry regulations, older harvest units might not contain as many snags and therefore should be weighted accordingly in the Lifeform modeling and impact analyses. Some of the previous harvested units did not have snag and leave tree requirements that are in effect today. Therefore, during modeling, the previously harvested units were not considered to provide suitable habitat until they reached a stand age of 10 to 20 years old.

Forest Health Modeling

In order to assess the impacts of HCP implementation on forest health, models were constructed based on fuel loading and insect damage potential relative to stand age, average diameter, and tree species composition. Output from these models were intended to broadly estimate how the landscape would respond to the assumptions made for varying harvest levels among the different landowners and vegetative conditions across the HCP area. Results were mapped to depict the variability in these risk factors on the landscape and to show the change of these risks over the 50-year HCP. The implications for species dependent on snags and CWD are that habitat potential is closely linked to conditions that increase the likelihood for fire and insect outbreaks. The modifying effect of wildfire on the density and distribution of habitat structural elements over the landscape is of course hard to predict, but could be a factor in the amount of suitable habitat available to these species in the future. Updating of the forest stand structure inventory and growth modeling on a periodic basis will assess any significant changes in the landscape as they occur. Plum Creek used this information to display and minimize the tradeoffs between provision for late successional habitat and economic risks due to forest health. The analysis also provided an opportunity to evaluate the cumulative benefits of conservation through a combination of Plum Creek's HCP and the Federal Northwest Forest Plan.

Increase of Snag Retention Targets on the Eastside of the Cascades Mountains

One mitigation measure in the HCP was to increase the snag retention targets within timber harvest units on the eastside Cascades. State forestry regulations recognize that eastside managed forests typically have a greater variety of selective harvests, compared to westside even-aged management. Selective harvests, combined with the greater natural snag recruitment potential of eastside forests due to fire, insects and disease, reduced the need for greater regulatory requirements for snag retention. Under the HCP, Plum Creek will increase the retention target above the state's requirement for these Eastside forests because much of Plum Creek's ownership provides transitional forest habitat between east and westside Cascades wildlife species.

Another feature of the HCP that increases snag retention on the landscape is the requirement that post-harvest snag levels be calculated excluding leave trees left within the designated riparian habitat areas along fish-bearing and perennial streams. This requirement ensures that snags are left in the upland portions of the landscape and are not allocated only to riparian areas.

Development of Sampling Techniques for Snags and CWD in the HCP Area

A mitigation measure was developed in the HCP to increase our knowledge of wildlife habitat elements within the various forest stand structures on the HCP landscape. An inventory field procedure was developed to collect data on snags, CWD, and understory vegetation during timber inventory updating on the company's lands. This information provides data on the abundance and density of snags and CWD in various size classes and decay stages. Understory vegetation data is taken in the form of percent cover for the three plant groups of shrubs, forbs, and grasses, in addition to specific berry and seed producing species. This information on specific habitat elements will be used to validate the assumptions (associations between the Lifeforms and the structural elements of forest stands) used in developing the HCP habitat approach.

Snag and CWD Opportunities in the HCP

In addition to the specific mitigation measures for snags and CWD, the HCP also contains mitigation measures for other species that benefit snag and CWD-dependent or associated species. These additional measures are generally in the form of timber harvest prescriptions and leave areas that contain snags and CWD.

The riparian strategy in the HCP was developed to not only protect and maintain the aquatic resources but also to provide habitat for those species that might use these areas as part of their life history and dispersal functions. The vegetative condition of these riparian areas in terms of canopy cover, tree size, and density are maintained as suitable northern spotted owl habitat. If these conditions are met or exceeded, some level of harvest in the outer zones of the riparian areas is permitted, but entry is generally limited and leads to retention of many of the snags and defective trees. Mitigation measures also address the maintenance of forested wetlands and protection of springs and seeps by retaining trees along their banks for erosion control and temperature moderation.

Timbered buffers are also provided in the HCP for talus slopes that maintain the biological integrity of the site for temperature moderation and a source of future CWD *(fig. 1).* Screening buffers are also maintained along open roads within the North Cascades Grizzly Bear Recovery Zone to decrease bear disturbance and mortality associated with human use of open roads. These screening buffers are maintained at a tree density adequate to obscure a grizzly bear within 100 feet of an open road**.** *Figure 2* shows a recently harvested unit that implemented a forested wetland prescription in combination with a grizzly bear screening buffer along a road that must be kept open to public use.

Figure 1—Post-harvest aerial photo of a talus slope buffer prescription from the Plum Creek's Cascades Habitat Conservation Plan. This mitigation measure provides upland snag and course woody debris retention widely distributed across the landscape.

Figure 2—Post-harvest aerial photo of a forested wetland buffer and grizzly bear visual screening cover along open public roads in the Plum Creek's Cascades Habitat Conservation Plan area. Retention of habitat structure in these settings provides additional benefits to cavity-dependent wildlife.

Larger protected areas are provided in the plan at specific spotted owl and northern goshawk nesting areas to support foraging areas near the nest or allow for dispersal and connecting corridors to adjacent USDA Forest Service lands designated as late-successional forest reserves. Some of these HCP protection areas will not be entered for timber harvest for 20 years as the surrounding areas on Forest Service ownership grow into more suitable owl habitat. Other areas can be selectively harvested, but vegetative conditions again must meet the canopy cover, tree size, and density criteria for suitable spotted owl dispersal habitat. Commitments to the U.S. Fish and Wildlife Service are to increase the percentage of spotted owl habitat on Plum Creek lands in the HCP area from 29 percent in 2006 to 55 percent in 2045.

All of these buffers and habitat areas provide the potential for additional snags and CWD in the landscape distributed among riparian areas and uplands.

Monitoring

Snag and CWD values are being evaluated in three areas. First, habitat conditions presently found in the landscape is evaluated. Second, post-harvest achievement of desired future conditions relative to snag and down log density is monitored. Lastly, the wildlife guilding assumptions used to relate wildlife species to HCP forest stand classes is being assessed.

Existing habitat conditions are being sampled across all forest stand focusing on snags, CWD, and understory vegetation. These data are being used to evaluate the presence of structural elements in the eight forest stand types described in the HCP area. Preliminary analyses indicate that this information will be useful in describing how these elements are distributed in the landscape by forest stand type *(tables 1, 2).*

Table 1—*Preliminary data from an ongoing timber stand inventory update project describing snag characteristics of stands in Plum Creek's Cascades Habitat Conservation Plan area, central Cascades, Washington.*

Stand structure[1]	No. of stands	Mean number of snags per hectare	Mean snag height (m)	Mean snag diameter at breast height (cm)	Pct hard snags[2]	Pct soft snags[2]
Stand initiation	17	1.6	6.4	56	39	61
Shrub sapling	68	0.8	4.6	53	5	95
Young forest	144	2.4	6.4	46	37	63
Pole timber	96	4.0	7.0	43	56	44
Dispersal forest	89	7.7	9.5	41	43	57
Mature forest	91	8.1	11.3	41	47	53
Managed old growth	7	4.8	11.3	38	37	63
Old growth	3	4.8	10.1	53	43	57

[1] Stand structures follow a successional sequence and are defined in Plum Creek's Cascade Habitat Conservation Plan (Anonymous 1996a).

[2] Hard snags are defined as decay classes 1 through 3, and soft snags are decay classes 4 and 5 (following the classification scheme developed by Cline and others 1980).

Table 2—*Preliminary data from an ongoing timber stand inventory update project describing down wood characteristics of stands in Plum Creek's Cascades Habitat Conservation Plan area, central Cascades, Washington.*

Stand structure[1]	No. of stands	Tons of down wood per hectare	Mean piece diameter at transect intersection (cm)	Pct hard logs[2]	Pct soft logs[2]
Stand initiation	17	15.8	25	17	83
Shrub sapling	68	18.6	25	13	87
Young forest	144	17.0	28	9	91
Pole timber	96	13.8	28	7	93
Dispersal forest	89	10.5	28	11	89
Mature forest	91	11.3	28	17	83
Managed old growth	7	8.5	31	26	74
Old growth	3	13.8	38	19	81

[1] Stand structures follow a successional sequence and are defined in Plum Creek's Cascade Habitat Conservation Plan (Anonymous 1996a).

[2] Hard logs are defined as decay classes 1 through 3, and soft logs are decay classes 4 and 5 (following the classification scheme in Maser and others 1979).

Post-harvest stands are sampled to determine if expectations with regard to the numbers of retained snags and down logs are being met. A random selection of harvest units is sampled by consulting foresters to quantify the leave trees retained in harvest units, following HCP guidelines. Results to date indicate that HCP implementation is meeting or exceeding targets. Compliance checks are also performed by the U.S. Fish and Wildlife Service and National Marine Fisheries Service, along with State agencies as part of state forestry monitoring.

The assumptions used in guiding wildlife species to the various forest stand types in the HCP landscape is being evaluated. A Plum Creek/University of Washington project is investigating bird use of HCP forest stand types by using point counts, territory spot-mapping techniques, and nesting/productivity indication indices. This research will help verify the habitat associations for permanent resident birds and neotropical migrants that use forest stands in the HCP area.

Summary

The Plum Creek's Cascades HCP is one of the most complex and comprehensive HCPs approved. The HCP is a landscape level ecosystem plan that was designed to work in concert with the Northwest Forest Plan for Federal lands to address multiple wildlife habitat issues across a large area of intermingled ownership. After 5 years of implementation, valuable data on species occurrence and habitat relationships are being collected. All this information is provided to Federal and State agencies and can be used by public managers and private landowners interested in developing HCPs or other landscape planning efforts.

Current knowledge and research in snag dynamics and cavity-dependent wildlife was used during development of the HCP. In addition to specific mitigation measures targeting snag and CWD issues, there are many ancillary benefits to species associated with these structural elements from other mitigation measures designed to address the needs of other species or habitats. Implementation, monitoring, and model testing are providing opportunities to work with Federal and State biologists to improve the HCP where needed.

HCPs provide substantive and meaningful incentives to private landowners to address a wide range of wildlife issues (including snags and course woody debris) while providing the long-term regulatory predictability needed for forest management. These plans also provide opportunities to improve knowledge and further our understanding of landscape processes.

Acknowledgments

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Management of Dead Wood: Perspectives of a State Forestry Agency[1]

Christopher P. Rowney[2]

A resolution adopted by the California Board of Forestry on July 20, 1887 (Raymond 1968) reads:

> Whereas, the Government and laws are totally inapplicable to forest lands, giving neither protection to the public domain nor to legitimate lumber industry, these laws are notoriously evaded and entries under them have been fraught with fraud and perjury. To carry on the lumber industry at all, fraud is really a necessity. Besides these defects, the land system in relation to forests makes no provision for a continuous supply of timber, nor does it give any attention to the necessity of preserving a due proportion of forest for the maintenance of springs and streams and climatic conditions favorable to agriculture....

This document was not the result of an epiphany in the past few years. But are laws better suited to their stated purpose today?

The 1887 resolution has elements of a continuing theme of the Board: providing for sustainable use of natural resources, protection of valuable public resources such as water quality, concern about appropriate implementation of regulations, and using a system of regulation that assures the continued viability of the timber industry in California.

Those are simple words, but exceedingly difficult tasks. Everyone wants something from California's timberlands. Fish and wildlife depend on it for productive and protective habitat, loggers depend on it for a living wage and job satisfaction, urban areas need a dependable supply of clean water, some environmentalists seek a religious experience, many desire recreational opportunities, and all of us depend on these lands for a steady supply of wood for an ever increasing population.

Since the Board of Forestry was formed in 1885, there has been a constant evolution of regulatory structure to address the widely varying demands placed on our timberlands. Initially, most of the emphasis was placed on wildfire suppression and reforestation. That focus shifted substantially in the late 1960s and early 1970s. Up to that time, the Board of Forestry was primarily a creature of the timber industry

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and reflected those priorities of assuring future crops of trees. As a result of a court decision, the Legislature changed the Board composition such that the majority represented the public and its interest in the management of timberlands. The Z'berg-Nejedley Forest Practice Act of 1973 (Public Resources Code §4511, *et seq.)* followed and clearly established that many resource values, such as water quality, aesthetics, and wildlife protection were important as well. The Act primarily provided that the productivity of California's forest lands be maintained and enhanced "while giving consideration" those associated natural resource values, and that language remains today (Public Resources Code §§4512, 4513). The focus, however, continues to evolve with a shift that elevates non-timber values.

As California continues to grow and more people are moving into the less populated areas of the state, demands on our forestlands grow as well—more for the associated values than for the timber those lands can supply.

The 1973 Forest Practice Act began a dynamic process of rule development, application, review, and adaptation that continues today. Today's California Forest Practice Program is comprehensive, prescriptive, and expensive. It is also accused of being unnecessarily burdensome and not founded in good science.

With the increased involvement of the National Marine Fisheries Service (NMFS) and the Environmental Protection Agency (EPA) in their enforcement of Federal laws, the California timber harvesting regulatory process, touted by many as the most stringent in the nation, has become more regulated. In the case of coho salmon *(Onchorynchus kisutch),* the NMFS has simply stated that the rules do not adequately protect the habitat of anadromous salmonids. In the case of compliance with the Clean Water Act, the EPA has concluded that the rules do not adequately address the problem of sedimentation. Environmental groups compared California's practices to those envisioned on Federal lands in the Pacific Northwest (i.e., Forest Ecosystem Management Assessment Team [FEMAT]; Anonymous 1993) and found them inadequate.

A founding principle of the Board was, and continues to be, to care for the landscape and its associated natural resources. The priorities of California policymakers in developing regulatory mechanisms in the management of both public and private land has changed significantly as the roles of ecological attributes are better understood. In California, up until the mid-1970s, the key for protection of those resources was in the area of fire prevention and suppression.

This was particularly evident in regulations adopted for control of harvests on non-Federal lands in 1948. One regulation required that any snag within a harvest area that was 16 inches DBH and 20 feet tall or more, had to be cut down. The purpose of that regulation was to reduce the risk of fires spreading to snags and throwing sparks for long distances.

That regulation remained in place until the mid-1970s. With the advent of more knowledge and concern about the effects of timber harvesting on avian species, particularly those listed under the State or Federal Endangered Species Act, rules adopted by the Board not only established minimum retention standards for specific species of birds, but provided that snags should be retained for wildlife habitat—despite the heightened market potential of that resource. Salvage of snags and other dead wood was essentially unknown in the 1940s and 1950s, and real market value was not present until the late 1970s. Today's regulations require snag retention. They may be removed only if required by the Director of the Department of Forestry and

Fire Protection and they are within 100 feet of main ridges suitable for fire suppression and identified on a Timber Harvesting Plan map, or if they are within 100 feet of roads and railroads. Other exceptions include safety hazards, disease or insect control, or when felling would not result in adverse impacts to wildlife habitat.

Emerging challenges are statute and regulations providing for exemptions for removal of dead and dying timber (Public Resources Code §4584; Title 14 California Code of Regulations §1038(b)). These exemptions are exempt from the necessity of preparing a Timber Harvesting Plan and interdisciplinary review. There is concern that such activities may be resulting in significant adverse environmental impacts, despite the underlying presumption, by both the Legislature and the Board, of insignificant environmental effects.

Over the past several years more attention has been centered on retention and recruitment of large woody debris (LWD) in and near watercourses. This is a radical change from earlier regulatory approaches to fisheries habitat.

I can recall going to a presentation by the Department of Fish and Game in 1973 with a number of forest industry people in Humboldt County. Included in the pictures presented was one of a stream with a large amount of wood in the channel, apparently preventing the migration of anadromous salmonids. The presenter then showed a picture after state crews had rehabilitated the channel. My supervisor, a forester, described it as an ecological desert. There was no wood in the channel and a tractor had been used to develop a relatively straight and diked watercourse. There is no question that harvesting in the earlier part of the century through the 1960s delivered massive quantities of wood debris to watercourses, probably in excess of that required in a healthy riparian system. The reaction, unfortunately, has resulted in problems we live with today in terms of biological and hydrologic problems and the mindset that dead stuff in the streams reduces fish habitat and enhances flood events.

In contrast to that presentation is one presented by the Department of Forestry and Fire Protection in an appeal hearing of a Timber Harvesting Plan at a recent Board of Forestry and Fire Protection meeting. A picture was presented that showed a large amount of LWD in a watercourse and trees that leaned into the watercourse. It looked as "bad" as the pictures used by the Department of Fish and Game almost 30 years ago, but those conditions were now characterized as demonstrating a healthy environment for fish and providing effective sediment metering for that watershed.

Although changes in agency perceptions of appropriate management of LWD in watercourses played an important role in interagency review of Timber Harvesting Plans, no regulations actually addressed that resource. The Board of Forestry made some initial rulemaking in the early 1990s to address the need for recruitment of LWD by requiring that at least two living conifers /acre greater than 16 inches DBH and 50 feet tall be retained within 50 feet of Class I and II streams.

The Scientific Review Panel, a result of an agreement between former Governor Wilson and NMFS, recently provided the California Resources Agency a report of its comprehensive review of the present Forest Practice Rules as they relate to the protection and enhancement of anadromous salmonid habitat (Rynearson and others 1999). That report recommended permanent retention of 10 trees of the upper 20 percent of the diameter distribution per 330 feet of stream channel within 50 feet of the transition line. That recommendation is included in a regulatory proposal considered by the Board during the winter of 1999-2000 for adoption.

The Board is also entertaining proposals that would enhance dead wood throughout the hillslope. Many people feel the Forest Service model described in the Forest Ecosystem Management Assessment Team report should serve as a basis for retention and recruitment standards. It is important to remember that most of those lands that the Board regulates are in private ownership. Thus, in order for the Board to craft regulatory standards, it must consider the issue of violating the constitutional protections against the seizure of private property without compensation.

From a regulatory standpoint, direct prescriptions for retention and recruitment are the subject of a great deal of commentary—too much or too little, depending on the interest of the person. Most importantly, regulations that are general by their nature are not well suited to address site-specific needs. The Board recognizes that comprehensive watershed assessment is the ideal direction to take. Near term solutions in the form of statewide regulations must give way to meaningful specific watershed analyses.

The laws developed to protect resources are inadequate if they are not implemented. That appeared to be the frustration of the Board back in 1887. Requiring something to be done simply because it is the best available technology or best management practice is insufficient if no one actually does it. It is even worse if, later on, it is found to be the antithesis of what is really needed.

Nearly three decades ago, the Society of American Foresters (SAF) defined forestry as “managing and using for human benefit the forestlands and natural resources that occur on and in association with forestlands, including trees, other plants animals, soil, water, and related air and climate” (Ford-Robertson 1971). Less than 2 decades later, SAF significantly changed the focus to “the science and art of attaining desired forest conditions and benefits” (Anonymous 1989). An element of the definition is to “sustain and enhance forest resources for diverse benefits in perpetuity.”

In the earliest stages of its rule-making efforts under the Forest Practice Act, the Board emphasized a species-specific approach to habitat management and protection. This is particularly evident in the Board’s regulations for owls, eagles, and ospreys, to name a few. Regulatory policy is shifting from that species-specific approach to a landscape-based approach to wildlife and watershed management. To be effective, such policy requires stakeholder understanding and support. This is best achieved through education and incentive-based approaches, although some level of prescriptive regulation is unavoidable.

As is evidenced by the broad array of dead wood values that were framed in topical presentations at this symposium, it is clear that dead wood is more than a simple residence for birds or habitat component for fish. The difficulty is applying this kind of information on lands. In a landscape consisting of competing resources, competing land uses, and even competing regulatory frameworks, there will be change in our regulatory process, but in all likelihood it will be compromise of some sort.

There are going to be changes in the Board’s view of appropriate forest management, but it is a continuation of thoughts that began with the Board in 1885. There is no question that some of those changes will reflect an increasing appreciation of the role of dead wood in a healthy ecosystem.

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Moving towards a New Paradigm for Woody Detritus Management[1]

Mark E. Harmon[2]

Abstract

Woody detritus has become an important focus of many scientific and management questions in forests. Perspectives of the role of this part of the ecosystem have greatly changed over time. Today forest managers are moving away from a "blanket" removal of all the woody detritus possible to retaining and even enhancing the amounts in forests. To understand how much woody detritus is required to sustain ecosystem functions, we need to develop a dynamic and specific objective-oriented approach. This can be based on existing data on tree mortality and decomposition, but these will have to be coupled with process and species responses to coarse wood quantities as well as a landscape perspective.

Introduction

In the last decade, woody detritus, particularly the coarse fraction, has become an important focus of many scientific and management questions. Although the role of this material in providing habitat and carbon cycling is generally understood, perspectives on its role in nutrient cycling are still evolving. Based on what is known to date, forest managers are moving away from a complete removal of all the woody detritus to retaining and even enhancing the amounts in forests. This leaves open the question of how much woody detritus is required to sustain ecosystem functions. Initially, this has been solved by the application of static minimum standards based on a set of general objectives, but in the future a more dynamic and specific objective-oriented approach should be developed. The increasing number of studies on tree mortality and decomposition are giving a global view of how these processes vary with forest type and climate. These data also provide the basis for a dynamic rather than a static approach to the management of woody detritus. However, to be successful, this perspective must be coupled with a detailed understanding of how certain species and ecosystem processes vary with the amount of woody detritus.

Woody detritus is an important component of forest ecosystems, reducing erosion and affecting soil development; storing nutrients and water; providing a major source of energy and nutrients; serving as a seedbed for plants and as a major habitat for decomposers and heterotrophs (Ausmus 1977, Franklin and others 1987, Harmon and others 1986, Kirby and Drake 1993, McCombe and Lindenmayer 1999, McMinn and Crossley 1996, Samuelsson and others 1994). As knowledge of these important roles in forest ecosystems has increased, the need to manage this material

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to maintain these functions has also increased. Although we are moving away from a period when woody detritus was given only economic, engineering, or safety considerations, we have not fully replaced this paradigm with a new one. In this paper, I outline what this new paradigm might be and point out the types of scientific knowledge that will be required to make it a reality.

Historical Perspective on Management: The U.S. Pacific Northwest Case

The old adage, "Those who ignore the past are doomed to repeat it," is sound advice. Thus, before describing what the future of woody detritus management might look like, it might be best to describe what has happened in the past. As forest resources have been harvested throughout the world, the attitudes toward that harvest and the value of those resources have changed with time. Although each region of the globe has had a unique development, there are certain trends they share. These general patterns can be illustrated by the historical trends in the U.S. Pacific Northwest, a major region of timber resource development, and one of the regions where woody detritus management has been rapidly changing.

The Unlimited Resource

The timber resources of the Pacific Northwest were initially regarded as limitless. Moreover, the timber resource was often viewed as a roadblock to "progress." This attitude had two consequences: low utilization standards with the highest quality wood harvested and the rest left to decompose, and a removal of forests by harvest or other means such as fire. Early this century some stumps were up to 6 m tall (Gibbons 1918), and stumps 3-4 m tall were not unusual (Conway 1982). Trees were cut this way to avoid butt rots and flair at the base of the trees. Reports at this time indicate > 10 percent of the stand volume was left in stumps (Gibbons 1918) with considerably more in the form of unharvested "undersized" trees. Between 1920 and 1930, stump height was reduced to 1-1.75 m, amounting to 6-7 percent of the total bole volume. In the 1910s the average diameter of logs left after harvest was 43 cm (Hanzlik and others 1917). During the 1920s it was common to leave logs < 35-56 cm diameter depending upon the length (Hodgson 1930). In 1910, the typical harvest of an old-growth stand would have retained 65 percent of the live woody organic matter aboveground as slash. This is close to the amount that would be retained on site after a catastrophic fire or windthrow with no subsequent timber salvage (Agee and Huff 1987, Spies and others 1988). Although woody detritus in forest ecosystems was not deliberately managed at this stage, it was certainly changing. In upland forest the amount of wood detritus increased at this time because the catastrophic disturbance rate was increasing as timber harvest increased (i.e., the mean fire return interval was 200 years, whereas timber was harvested at a rate in which the mean return interval was > 100 years). This change increased the input of woody detritus and therefore increased the average landscape level of woody detritus above those of the historical average *(fig. 1).* In contrast to the upland system, in the riverine system woody detritus was being removed and burned to improve safety and transportation, effectively increasing the decomposition rate-constant. This lead to a decrease in woody detritus stores in riverine systems at the time that upland stores were increasing.

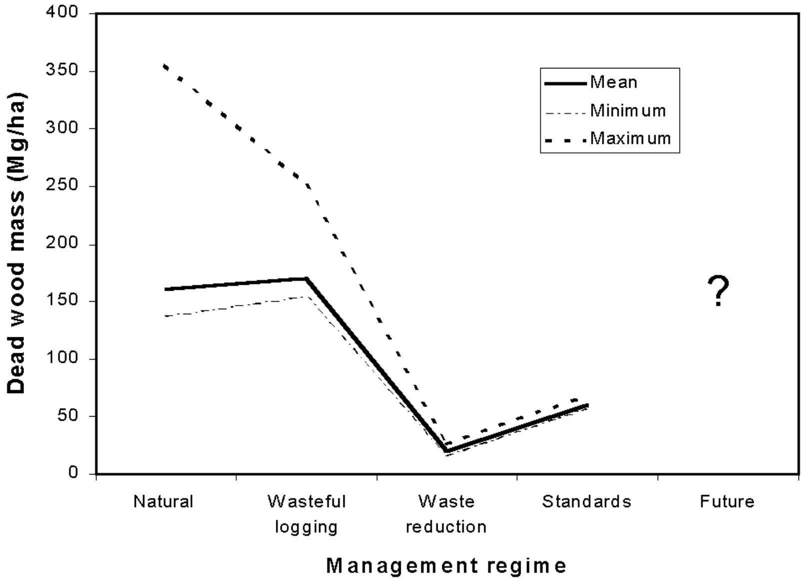

Figure 1—Hypothetical amounts of woody detritus found in upland landscapes during various stages in development, using the Pacific Northwest as an example. The values were derived using a simulation model (similar to the one described in *fig. 2*) and parameterizing it by using data from Harmon and others 1996. The heavy line represents the mean, whereas the light lines indicate the range over succession.

Woody Detritus as Waste

The next stage of development was largely a response to the previous one. As the timber resource was removed deliberately or by accident, it became scarcer and therefore more valuable. What was originally an unlimited resource was then seen as a limited resource that required more efficient management. Forests were therefore seen to be in the need of protection from natural (wind, fire, insects, fungal) and man-caused disturbances (fire, agricultural clearing). Moreover, utilization standards that removed only the "best" volume became viewed as wasteful. Improvements in utilization standards by the 1940s lead to a five- to tenfold drop in stumps height to 0.6 m (Poole 1950). More significantly a trend of removing smaller diameter trees and tops started with a minimum of 30 cm in the 1930s and steadily decreased to 13-15 cm today. The forestry literature at that time in the Pacific Northwest was full of examples of economic waste. For example, Hodgson (1930) calculated that the mass of sound wood retained after harvest in western Oregon and Washington forests during the 1920s exceeded the entire amount cut for pulp over the entire U.S.! As another example, re-logging of former harvest units was economically viable for several decades (Hodgson 1930).

Although changing to a more efficient form of harvest made economic sense as resources became scare, it also had some very important consequences that did not make ecological sense. The earlier harvest practices were viewed as wasteful, and therefore woody detritus became the symbol of that waste regardless of its origin. Forest utilization standards were not only improved to reduce this wastefulness but also the symbol of that waste had to be removed. It was the latter step that led to potential ecological problems, but these were not anticipated. Rather, many justifications concerning sanitation, productivity, fire protection, and logger safety that went far beyond changing wasteful practices were developed. These justifications took on a life of their own even though they often had no basis in fact. For example, pathogens were thought to spread from dead trees, but with very rare exceptions this was not true as the pathogens lived primarily on living trees (Cramer 1974). Fire-killed trees and windthrows had to be removed because pathogens and insects would threaten the surrounding living trees. Bark beetles became a general rationale for dead tree removal, despite that many species of trees (e.g., *Tsuga heterophylla* and *Thuja plicata*) are generally not attacked by these pest insects. Even those trees that do support these insects *(Pseudotsuga menziesii)* often do not form good habitat for beetles that cause extensive and long-term infestations (Powers and others 1999). Snag felling was extensively practiced to promote safety, and yet many of the areas in which this practice was carried out had vanishingly low probabilities of snags damaging buildings, vehicles, or humans (at least there was no detectable increase in incidents when the practice was stopped). Logs were removed to ease tree planting, although the major problem in slowing planting was small and not large slash material.

The ultimate expression of this phase of development occurred when not only the wasteful practices were stopped and recently killed trees that could be economically utilized were removed, but when woody detritus that could not be utilized for anything except firewood was removed and eliminated by burning. This era of piling unmerchantable material (PUM) and yarding unmerchantable material (YUM) represented a phase in which the existence of woody detritus was not to be tolerated even if it cost a great deal of money to remove it. As such it represented waste removal carried to its illogical extreme. It also led to a landscape in which woody detritus was far below any historical level *(fig. 1).*

Ecological Functions

Not only did PUM and YUM practices have an economic downside associated with the cost of yarding and burning, they started to have impacts on the ecological system. Research started in response to these practices that revealed many of the functions we take for granted today (Harmon and others 1986, Maser and Trappe 1984). The search also began for a more balanced way to deliberately manage woody detritus in the ecosystem. The first idea was to develop minimum standards for the amount of woody detritus to be retained in harvested units. Minimum standards were set a number of ways, but most frequently in the Pacific Northwest they were based on the minimum numbers of pieces or volume found in old-growth forests (Spies and Franklin 1991). To serve certain functions it was also recognized that minimum diameters and lengths needed to be provided. While the emphasis on upland systems was on the time of harvest, a point when woody detritus could either be enhanced or retained, the focus on riparian systems was on restoration with wood actually either being added artificially from outside the system or produced naturally in designated riparian buffer zones.

Although minimum standards are an improvement in terms of retaining ecological functions, they also have certain problems as currently practiced. First, while they have the potential to increase woody detritus above the level of the previous era, they also have the effect of homogenizing the amount of woody detritus over space and time. As woody detritus in a natural system is highly variable it is not clear what this homogenization implies for many ecosystem functions. Minimum standards are easy to set and enforce but often are difficult to apply—how should stages of succession or forest types be managed in which the amount of woody detritus is naturally lower than the minimum? Should wood be added to make it comply with the standards? These questions often confront the manager trying to apply one-size-fits-all standards. Second, the minimum standard approach is mute on how the minimum should be determined. Ideally, this should be determined by the tradeoff between ecological and economic gains and desired outcomes (Wilström and Ericksson 2000). However, in practice this has been settled by balancing the amount of woody detritus against the economic cost. This system inevitably leads to the factor that can be quantified (i.e., economics) becoming more important than the qualitative factor (i.e., we need some more woody detritus). Third, because the management intervention for the upland system occurs during harvest, minimum standards lead to static management of a dynamic entity. Thus, once the minimum standard has been met, the tendency is to assume that ecosystem functions will be provided despite that the system is very likely to change over the decades between harvests.

“Morticulture” and the Elements of a New Management System

Clearly a paradigm that moves beyond minimum standards needs to be developed. But how will it be developed and what will it look like? We might start with the name of this new system and see where that leads us. Suppose in the future there will be a “morticulture” as well as a silviculture. Although I often offer this name in jest, it does have some serious points in its favor. It emphasizes the culturing of something, in this case woody detritus. As with silviculture it would meet future needs, but instead of the type of logs to be harvested, it would deal with the methods to produce woody detritus structures for ecosystem function. It would have a similar attitude about manipulating stand structure and, as in modern silviculture, acknowledge the dynamic nature of the system being managed. And morticultural practices would not be implemented unless the ecosystem response was exactly understood (just as in silviculture, methods should not be applied without trying to reach some goal in terms of species mixtures, forest product markets, etc.). In addition to these obvious parallels, morticulture should take advantage of past silvicultural experience. In fact its implementation should be considered in close conjunction with silviculture and not in isolation. The next section outlines in more detail some of the features of this new system.

Linking Live and Dead Trees

Although developing a viable morticulture will require new knowledge, in many cases it will require that we apply what we already know. For example, we already know that live trees eventually form dead trees, but it is amazing that this dynamic is often missing from current forest management thinking. Thus, the current tendency is to use wood produced from the old-growth stand at the time of forest conversion and harvest to meet the future needs of the system. Unfortunately, the new plantation forest system does not have the capacity to maintain this amount of woody detritus unless it is modified considerably in terms of rotation length and fraction of live trees retained (Franklin and others 1997, Spies and others 1988).

A similar disjunction occurs between standing dead trees (i.e., snags) and downed dead trees (i.e., logs). Clearly snags eventually fall to the ground to become logs, although some live trees fall to become logs without first becoming snags. An examination of management plans, inventories, and even the scientific literature indicates that there is both a significant failure to link snags and logs and to link live and dead trees. Yet, they are clearly all part of the same overall system. One way to functionally link these forms of wood is to use a common currency to examine their state and dynamics. The actual units used may differ depending on the objectives, but the current tendency to compare, for example, volume of logs to numbers of snags is unnecessarily reinforcing their separation.

The Dynamic Wood Pool

Managers of woody detritus currently tend to think about woody detritus management in static terms. Rather than ask at which rate woody detritus is created or lost, they tend to think about the amount that should be there. This is another case where we already know the processes that control woody detritus dynamics, but we are not applying this knowledge. Clearly, we need to learn more about the processes of mortality, disturbance, decomposition, fire consumption, and movement, but I maintain the most significant problem is switching from a static to a dynamic perspective.

Mortality is the process that creates woody detritus. It can occur by natural causes or by human-related causes. It can occur as single parts (e.g., branch pruning), as single individuals, or as entire stands (i.e., as landscape units). Forest management in the past century has focused on how to lower mortality rates via thinning, fire protection, etc. Ironically, the next century of forest management may be occupied with how to increase mortality when and where we want it. Despite the foresters preoccupation with reducing mortality, it is surprising how little is known about the actual rates of mortality in forests (Franklin and others 1987). This lack of knowledge may have been caused by the fact one needs to observe a population over time to determine rates and causes, although some stand reconstruction methods can give rough approximations of long-term rates (McCune and others 1988). Mortality rates are commonly thought to be highest in older forests (shades of our old friend waste reduction?), but they actually tend to be highest during the self-thinning stage of succession. For the forests that have been studied, old-growth rates appear to be one-third to half those of the self-thinning stage (Franklin and others 1987). There is also a tendency to only consider self-thinning in models of mortality, but this too is a mistake. Trees are often killed by causes unrelated to density such as wind, ice damage, insects, pathogens, and sometimes accidents (e.g., the second highest cause of death in Pacific Northwest forests is crushing by another tree or snag [Franklin and others 1987]). At the continental scale the tendency is for mortality to increase with productivity, although the cause of this relationship is not clear. Tropical forests have the highest mortality rates (0.0167 yr^{-1}) followed by deciduous (0.012 yr^{-1}) and then evergreen forests (0.01 yr^{-1}) (Harmon and others 2001).

Although disturbances such as fire and timber harvest obviously cause mortality directly, they also increase the chances that the surviving trees will die (Franklin and others 1997) because survivors are exposed to increased insect attack and/or to wind damage. While often viewed as a waste, this might also be an opportunity if increasing woody detritus is the management objective.

Decomposition is the fundamental process that regulates the loss of woody detritus. Although many insect species are associated with this process, basidiomycete fungi are probably the most important wood decomposers. Many factors control the rate of wood decomposition, ranging from the chemical and physical nature of the wood, to decomposers involved, to the environment at the micro- and macro-levels. This leads to a very complicated pattern of decomposition that is variable over the scale of meters. In northwestern Russia, for example, one can find logs under moss mats that are waterlogged, next to stumps that have optimum moisture, next to snags that are too dry to decompose except in their lowest meter of height (Krankina and Harmon 1995). There have been some attempts to measure the rate of the decomposition process over time (Harmon and others 1999, 2000), but these are relatively rare today. The majority of studies of woody detritus decomposition use a chronosequence approach that substitutes space for time. There is a great deal of data on decomposition rates of wood relative to mortality. On the macro-scale decomposition rates decrease from tropical (0.176 yr^{-1}) to deciduous (0.080 yr^{-1}) to evergreen forests (0.032 yr^{-1}) (Harmon and others 2001). Deciduous shrublands of the tropical zone appears to have the highest decomposition rate-constant, possibly due to the presence of termites. Although tropical forests have the highest decomposition rate-constants of any major biome, the distribution of values appears bimodal with a peak at < 0.04 yr^{-1} and another at > 0.12 yr^{-1} (Harmon and others 2001). This may be a reflection of two groups of species: one containing compounds toxic to fungi and insects in their heartwood and a second group that has little decay-resistance. In contrast, evergreen and deciduous ecosystems appear to have unimodal distributions of decomposition rates.

Fire consumption is another process that removes woody detritus. This process is highly variable and likely to change from ecosystem to ecosystem and even from fire to fire. Past research indicates consumption of woody detritus increases as moisture and piece diameter decrease, and as the degree of decay increases (Brown and others 1985, Rienhardt and others 1991). It is also clear that in most situations the consumption of large woody detritus is linked to consumption of the forest floor. The reason appears to be related to the extremely loose packing of woody detritus. To burn there must be a positive feedback of energy between pieces; and given the distance between large pieces of wood, this feedback is very low. Therefore, for coarse wood this positive feedback is with the underlying forest. This is important because it means that without deep forest floor layers, large pieces of woody detritus will not be completely consumed even when the moisture content is extremely low (similar to attempting to burn a single dry log in a fire place without another log or finer fuels).

The nature of the fire can also determine future decomposition rates. The classic idea is that charring slows decomposition, but this is probably only true for wood that is in the intermediate stages of decomposition. Fire charred trees are typically quite attractive to decomposers such as insects, many of which specialize on this form of mortality. Wood that has been fully colonized by decomposers is also likely to be little affected by charring, although increasing light absorbance is likely to heat the wood and lead to faster biological activity. Charring seems to only slow decomposition in logs that have the decayed portions fully removed, thus eliminating the normal sequence of colonization. Finally, it is often stated that fires removed much of the woody detritus prior to fire protection efforts; therefore, after decades of fire suppression current levels of woody detritus are artificially high. Perhaps, but these same fires would have killed trees that replaced the dead ones they consumed.

Given the ratio of dead to live trees observed in most forests (0.05 to 0.30 on a mass basis), very little mortality would be required to offset these losses (Harmon 1992). This may be the reason why two fire regimes in Oregon that differed fourfold in the frequency of fires had very similar amounts of woody detritus (Wright 1998). Those differences that did exist were more likely caused by environmental differences that lead to an increased rate of decomposition in the more frequent fire regime.

All these process rates vary with time, a dynamic that causes woody detritus to undergo changes over succession. Although there are undoubtedly many patterns of change after a disturbance, a few common patterns can be created by varying: the interval between disturbances, the amount of wood removed by the disturbance, the mortality rate, and the decomposition rate. The simplest case is for old-field succession where both live and dead mass start at 0 *(fig. 2).* In this case live and dead mass accumulation parallel each other. A more complicated situation occurs after a catastrophic natural disturbance. Assuming the disturbance removes a minimum of wood (e.g., wind throw), woody detritus at the time of disturbance is equal to former live biomass and the dead wood mass just before the disturbance. This peak is followed by a monotonic decline to a steady-state mass that is determined by the mortality and decomposition rates. When the disturbance removes a fraction of the woody mass (e.g., timber harvest) the quantity right after the disturbance can range anywhere between zero to that found after windthrow. In the example given in *figure 2,* the woody detritus mass declines below the steady-state value and then increases to this level. This is because the replacement of woody detritus lags behind decomposition in the middle stages of succession (Harmon and others 1986, Spies and others 1988). Perhaps the most complicated case is when forests are converted to intensive, short-rotation forestry. Here the live mass does not recover to the steady-state level and a large fraction of the mortality is removed as intermediate timber harvest in thinning and salvage. This leads to a decrease in the store of woody detritus to a value much lower than the steady-state value.

Response Functions

Knowing the dynamics of the woody detritus is not sufficient for deciding how much woody detritus is adequate. This requires knowledge of how various organisms or ecosystem functions vary with the amount and arrangement of this material. Unfortunately, this is probably the weakest portion of the science behind morticulture (and the hardest type of question to answer). The first problem is that we have tended to examine ecosystem and habitat functions either with or without woody detritus. But what we really need at this stage is a continuous response. Although there are few examples of continuous response functions, some do exist. Butts and McCombe (2000) examined the response of salamanders in western Oregon to the presence of woody detritus *(fig. 3).* They found that the abundance of some genera (*Aneides* and *Ensatina*) was highly correlated to the volume of woody detritus present, while others were completely indifferent *(Taricha).*

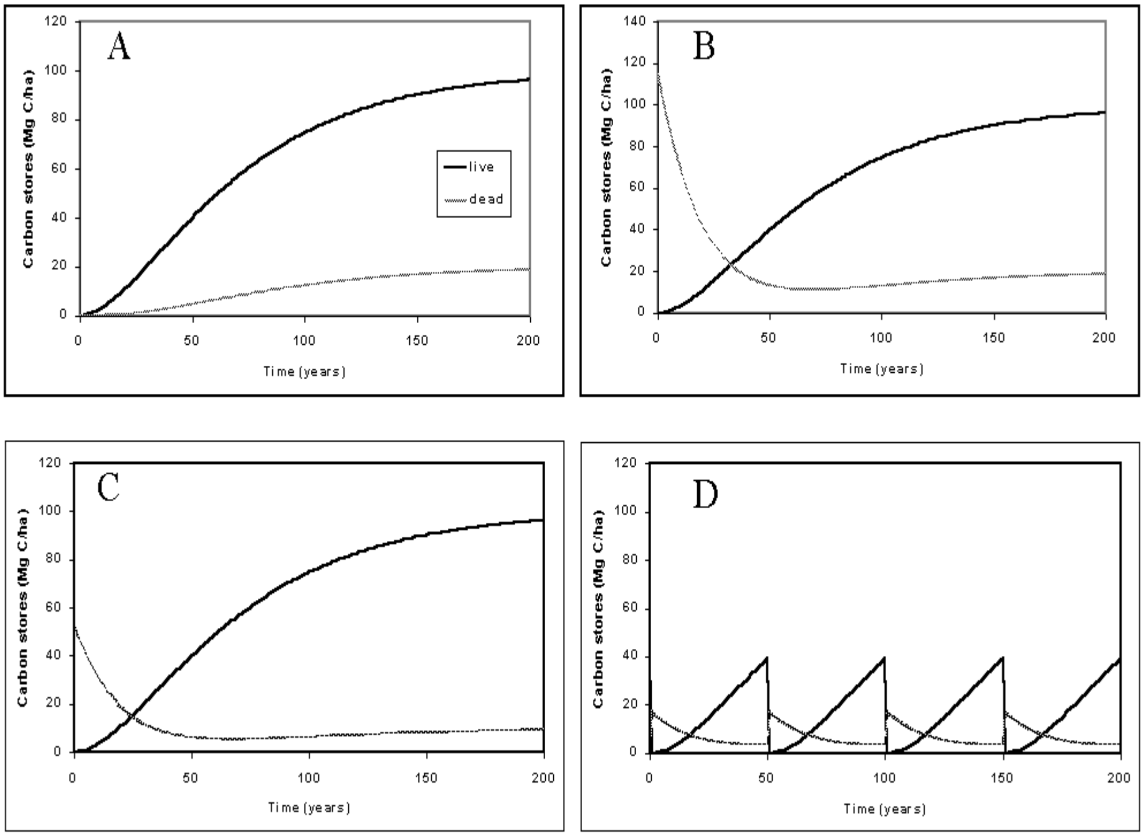

Figure 2—Hypothetical woody detritus stores relative to live woody stores for various management regimes. Stores are from a simple simulation model that uses a Chapman-Richards function to simulate live biomass and determines woody detritus mass from mortality from disturbances and regular death from competition, etc. as well as losses from fire and decomposition (Harmon and others 2001). For comparative purposes, woody detritus stores have been set relative to live woody stores and the maximum live woody stores were set to 1. A) old-field succession with no woody detritus at the start, B) succession after a natural disturbance that leaves all the woody detritus, C) a single clear-cut without subsequent harvest, and D) multiple harvests every 50 years with salvage of half the mortality.

From a theoretical standpoint, the expectation is that different ecosystem and habitat functions would have different responses to the amount of woody detritus *(fig. 4)*. A relatively small volume of wood might fulfill some functions, such as insect habitat, as long as the right species, size, and decay stage are provided. One might expect this type of response from any species with a small size, high reproductive rate, and high vagility. Vertebrates on the other hand might require larger volumes of woody detritus, in part because of their larger individual size, but also because they may require more connectivity of the wood itself to serve the function required (e.g., travel corridors). Some response functions might increase to a saturation point, whereas others might reach an optimum above which the function decreases. A possible example of the latter might be the response of fish to increases in woody detritus abundance. At first habitat quality might be increased; however, with too much woody detritus in the stream movements, food production and other factors might become limiting. The same might be true for nutrient cycling. Adding wood initially might increase the addition of nitrogen via asymbiotic fixation and might provide habitat for some mycorrhizae. But at some point woody detritus would tie up too many nutrients and cover too much of the forest floor so that plants might have limited places to establish. Although all of these are theoretical responses, they indicate range of types one is likely to see in nature.

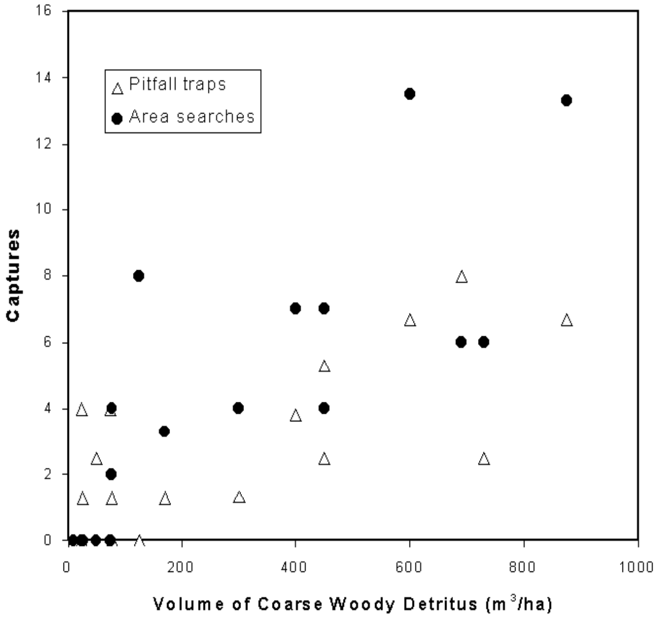

Figure 3—The response of ensatina salamander (*Ensatina eschscholtzi)* abundance to coarse woody debris volume (Butts and McCombe 2000).

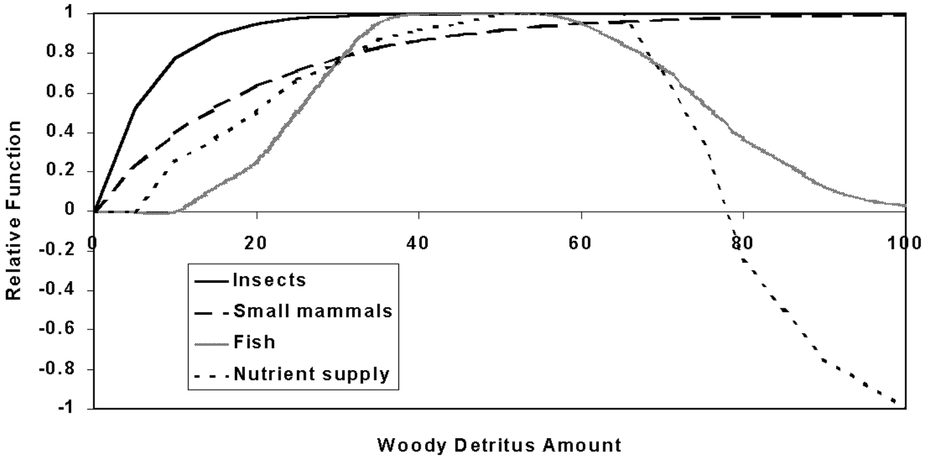

Figure 4—Hypothetical examples of species and ecosystem response functions to changes in the abundance of woody detritus. Note that both scales are relative, with the response function having a maximum of 1.0 and a minimum of –1, and the woody detritus scale ranging from 0 (no woody detritus) to 100 units of mass or volume.

Compensatory Factors

It would be a simple world indeed if we could treat responses to woody detritus in isolation. In reality the woody detritus resource interacts with others to determine the overall function of the ecosystem. To some degree these interactions might compensate for a decrease in woody detritus. For example, bacteria in woody detritus undoubtedly fix nitrogen that eventually becomes available to plants. It stands to reason that removal of this woody detritus would therefore decrease nitrogen inputs, but this might be compensated for by symbiotic nitrogen fixation in plants or lichens. Unfortunately, the same zealous attention to decreasing waste and increasing productivity of merchantable volume that has lead to the removal of woody detritus has also lead to the removal of both these symbiotic forms of nitrogen inputs.

Perhaps the more complicated question to answer is why other types of structures may or may not compensate for woody detritus. For some organisms, such as insects and fungi, this compensation is easily determined given that they often require woody detritus to fulfill certain life stages (Jonsell and others 1998, Renvall 1995, Rydin and others 1997). For others such as small mammals there may not be such a clear obligate relationship. If woody detritus serves as cover for small mammals, then another form of cover might be able to compensate for a lack of woody detritus. This suggests that in addition to developing response curves, we must understand what exactly the woody detritus is providing the organism or ecosystem. If there are no other ways to provide this function, then the amount of woody detritus is crucial. If on the other hand other structures or processes can provide them, then we may be more flexible in the amount of material retained.

Spatial Considerations

The final element to forming a new management paradigm for woody detritus management involves spatial arrangement. This can be at the level of pieces, stands, and landscapes. At the landscape level the first consideration might be whether the process or habitat provided by woody detritus is ubiquitous or restricted to certain locations. If it is ubiquitous then keeping a minimum level throughout the landscape may be adequate. An example of a ubiquitous process might be nutrient cycling, as it is continual regardless of the amount of woody detritus. If the habitat is restricted, the connectivity to other similar habitats or locations must be considered. If the species using woody detritus habitats have a high reproductive capacity and are vagile, spatial distribution may be of minor concern as long as the habitat appears somewhere each year (Jonsell and Norlander 1995, Jonsell and others 1999). On the other hand, for species with low reproductive capacity and restricted movements, one may need to carefully design where and when the woody detritus habitat occurs in the landscape. In addition, metapopulation dynamics may need to be considered (Hanski 1991). This problem might be addressed by providing stable areas in which populations dependent on woody detritus are kept high and can serve as sources to the surrounding, lower quality, and shifting habitats that are population sinks. While the latter are temporary, they would function to keep the overall abundance of the organism high at the landscape level. Metapopulation structure considerations may be influenced by the direction from which the landscape is being developed. In regions that have a great amount of high quality habitat, one might be able to design a self-sufficient landscape of source and sink populations. This will not be the case if restoring woody detritus functions to a “degraded” landscape is the goal. In this case, one might have to locate source populations outside the landscape of interest or create the woody detritus habitat and then wait for the chance dispersal of the desired organisms.

Although the bulk of recent ecological thinking about the spatial dimension has been on the landscape level, spatial considerations may also influence the function of woody detritus at finer levels of spatial resolution. If the primary function of downed woody detritus for small mammals is as protective cover from predators, the connectivity of individual logs might be important. One would hypothesize that the greater the connectivity of pieces, the lower the exposure to predation. Unfortunately, there are no studies that I know of that have looked at this problem from a theoretical or empirical perspective. Another question involving the spatial distribution of logs involves the effect of logs on soil forming processes. Tinker and Knight (2001) asked how long it takes logs to influence the entire soil surface. In lodgepole pine forests they found that it depends on the woody detritus management regime, with natural disturbances having a much shorter "log-rotation" time than current intensive forest practices. Interestingly, they found that minor modifications of current practices would shorten the log-rotation time to that observed for natural disturbances. Further work along these lines might add a great deal of insight into the long-term function of woody detritus in ecosystems.

Integration

Given these elements, how might this new paradigm of morticulture work? It would probably start by answering the question of which species or processes are to be maintained, restored, or otherwise managed *(fig. 5)*. Then the target levels for these functions should be determined. Before assessing the amount of woody detritus to be maintained or added to meet this functional target, the landscape context for the management action should be assessed. Are there limitations of populations or processes that would limit the desired response? If not, a plan to add wood would be designed to maintain the desired level. But if there are landscape limitations, then these should be addressed before planning at the stand-level proceeds. The ability to circumvent these limitations will probably be highly dependent on the given landscape; in some cases the particular patch treated might be part of an overall plan to reduce these landscape-level limitations. The plan to produce a given amount of woody detritus would have to be dynamic, linking the live trees and the different forms of dead trees so that there is compensation for losses caused by decomposition and fire. The plan would then be implemented and might consist of several interventions. Finally, the results of the action should be monitored for effectiveness (not just implementation), and a true adaptive management system should be put in place. The latter system will have real costs in money, time, and training, but will be necessary to really assess if things are working as anticipated.

This paradigm is admittedly a "fine filter" approach that emphasizes small scale processes and patterns. There is no reason, however, why it could not be coupled with a "coarser filter" landscape level view of the system. In fact the assessment of the landscape context would probably be the most logical point to reconcile these two perspectives.

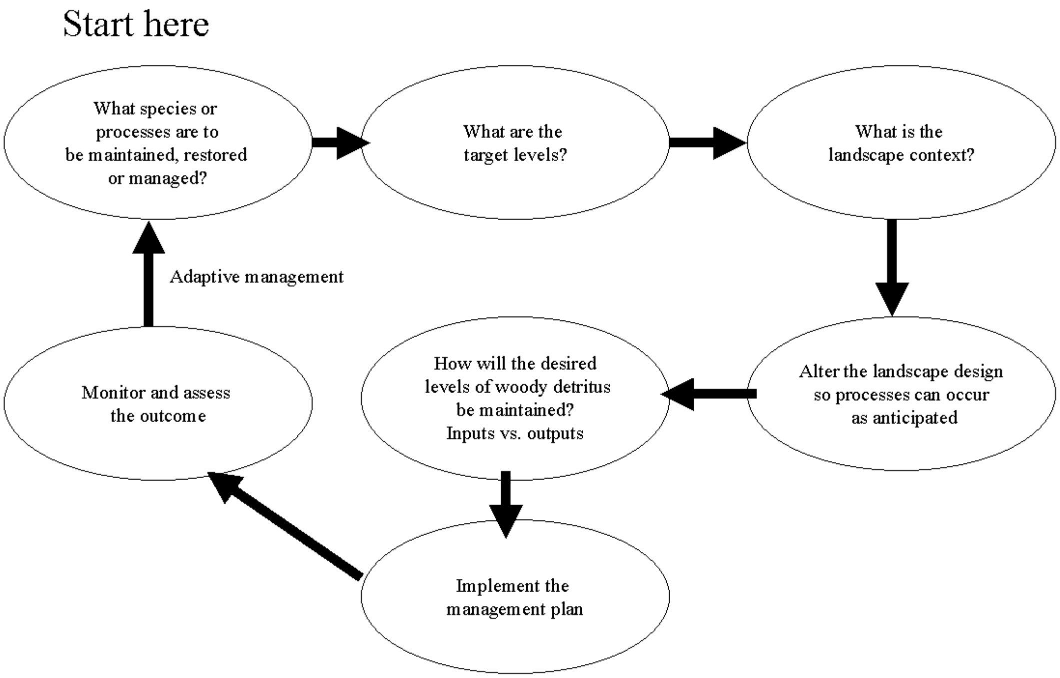

Figure 5—Integrating the elements of a new paradigm for woody detritus management.

Science Needs

Despite the need to improve our understanding of woody detritus dynamics in terms of mortality, decomposition, and consumption by fires, we already have enough knowledge of these processes to make reasonable projections of temporal dynamics at the level of stands. The same cannot be said about the response functions that are required to match the amount of woody detritus to the expected level of functionality at the ecosystem or landscape level. Clearly science needs to make major progress in this arena within the next decade if we are to see a new management paradigm take root in the near future.

Unfortunately, this is difficult research. In some cases it will be long term. For example, we have made many assumptions about the irrelevance (and relevance) of woody detritus in the nutrient cycles of forests. But very few of these assumptions have actually been tested. Perhaps it is time they are tested. Equally problematical, but perhaps easier to solve in the short term, is the specific link between woody detritus and specific organisms (e.g., is it a nesting site, transport corridor, food source, etc.?). We need to be able to establish these relationships if we are to have any faith in the response functions that are generated. The design of experiments that actually test the response of various organisms to the abundance of woody detritus will be harder but by no means impossible. This might be conducted using existing gradients in wood amounts, or it could be done in manipulative experiments where wood is either added or removed. One complicating factor is the ability of organisms to disperse between these treatments. Adding woody detritus to systems that are depleted might not result in a response if the organisms cannot find or disperse to these locations. Conversely, removing woody detritus in a landscape with an abundance of this material might not result in a decline if the treatment area is too small. Finally, we need to understand the historic and present dynamics of woody detritus at the landscape scale. We are beginning to understand these dynamics at the level of forest stands and other landscape elements such as streams. We must build up this understanding to the landscape level so that we can predict how managed landscapes differ from historical ones.

Conclusions

We have made progress in the last several decades in the management and understanding of woody detritus. Although the creation of minimum standards has been a useful first step in acknowledging the ecological function of woody detritus, it is not the ultimate solution to the problem. Rather, we need to develop a long-term, broad-scale view that is dynamic and that includes everything from proto-dead trees (live trees) to snags to logs to highly decomposed material that functions as soil organic matter. We also need to move away from arbitrarily setting amounts to a system based on the response of specific ecosystem function and species. This will be challenging to scientists and managers alike, but will be necessary if we intend to preserve, conserve, and restore the role of woody detritus in our forested landscapes.

Acknowledgments

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Symposium Synthesis

Dead Wood Management Issues and Opportunities: Future Directions[1]

Ann M. Bartuska[2]

Introduction

October 1999 marked the 50th anniversary of the Sand County Almanac, and with the associated celebrations has come a heightened awareness of the Leopold Land Ethic.

The array and depth of the presentations at this symposium underscores the increased understanding about dead wood in many forms. I am impressed by the collaborative presence of both managers and scientists. In his opening remarks, Jack Ward Thomas challenged the group when he said: "All that you folks have presented is only useful if synthesized and communicated." In my remarks I have tried to provide some broad themes within which the presentations at this conference are linked. I also have tried to capture issues and opportunities, which can provide some directions for the future.

Where Is the Dead Wood: Current and Future?

We are concerned about all the forests of the West, not just the National Forests or Federal lands. At regional and landscape scales, solutions to land management problems can only be accomplished by considering all lands. A risk-mapping project is one that identifies areas where mortality from insect and disease outbreaks link with fire-risk areas at the national and regional scales. The presence of dead wood (from mortality) and fuels (from dead wood) is the critical element for assessing risk. Using this information for management decisions will involve both ecological and social considerations.

Landscape or site: what intensity of sampling is needed? We heard from several presenters about possible approaches. I suggest we need to take a step back and about the level of information we need and with what degree of certainty.

Forest Health Monitoring/Forest Inventory and Analysis programs may provide a template that may be good enough at landscape and watershed-scales—although tree-centric, they are open to expansion of methodology. More importantly, their infrastructure and basic system are funded and incorporate all forested lands. Wildlife

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[1] An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

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biologists are finding this system useful in habitat assessments, and measurements to assess floristic ground-cover are being evaluated.

The model development presented in several sessions is really exciting. I was struck that these science-based systems are being designed with managers in mind. We must be smart to ask "at what scale is the model designed to provide information?"

What Role Does Dead Wood Play in Ecosystems?

The ecosystem arena is where most of the work seems to have been done and where the understanding is the most comprehensive—spanning physical, chemical, and biological processes. The science presented provides a sound foundation for management.

Jack Ward Thomas made a strong plea that it is time to integrate and synthesize. This integration must be across disciplines and ecosystems. One speaker was justifiably proud of getting wildlife biologists and fire managers together. I suggest that entomologists, pathologists, and silviculturists also need to be at the table in order for planning to be most effective. Silviculturists, in particular, should become a wildlife biologist's best friend.

Synthesis across ecosystems is overdue. In this way, we can identify the underlying patterns and delineate clear ecosystem-specific patterns.

How Do We Manage with Dead Wood?

I would suggest what we really need to do is manage with disturbance! As Mark Harmon suggested, we should "manage dynamic systems."

We must learn to manage with uncertainty. Our plans and analyses must recognize that we cannot and will never be 100 percent certain, and in fact, perhaps 50 percent is good enough. As scientists and as managers trained in the academic tradition, we are caught in a "$p = 0.01$" paradigm. The fact that uncertainty exists in science and in functioning ecosystems should be communicated to policymakers.

Can we focus on the structure and assume the other components (fauna, invertebrates, insects, etc.) will fall into place, or do we manage for each of the components separately? This is an issue that both scientists and managers need to address and resolve or we will continue to chase the parts.

Missing Pieces

The work presented at this conference has addressed the structure, function, and composition of dead wood in the ecosystem. However, ecosystem management identifies three interlocking components: ecological, social, and economic. Both Aldo Leopold and Gifford Pinchot recognized the importance of integrating ecological and social values.

The social and economic components of ecosystem management were generally missing. Where are the social scientists? The social values were touched on in some papers. For example, Bob Naimann made the link that woody debris provide a source of insects, which in turn is the basis for recreation fisheries. A landscape with a lot of dead trees visible may not be what the visiting public wants. However, through communications with the public, they may understand and accept widespread mortality caused by natural events.

The role of dead wood in the carbon budget, especially carbon sequestration and slow release processes, was incompletely addressed. Hennen's question about the ecological role of the longevity of standing dead yellow cedar may have its answer in the systems equivalent to long-term carbon storage.

There was a surprising absence of references to non-native, invasive species. The current heightened concern about their spread and introduction is touching all aspects of land and water management. One obvious concern is the effect on predicted patterns of mortality from insects and disease. We have good knowledge on the population dynamics of the major forest insects and diseases, and the geographic patterns using the greater than 50 years of annual pest surveys done by the Forest Service and the States. We do not have knowledge of the biology and impacts of recent introductions.

Considerations for Future Work

Standardization of methods is essential and will be more effective if the scientific and management community does this; otherwise it will come from the top. Scale-specific monitoring systems must be established. Is there such a thing as too much dead wood?

Rapid response to disturbance events at all scales should be developed. There are well-established policies and procedures when there are fires, but not with other large-scale disturbances.

Synthesis within and across scales is a major gap in our analyses and must be pursued. Are there universal truths or a lot of landscape-specific patterns? Information must be communicated in useful forms to managers and to the public.

My closing thoughts echo those of Jack Ward Thomas: we all must assume some responsibility when science is brought to the management table. As scientists, we should continue to strive to better understand the structure, function, and composition of ecosystems. However, when conveying this information to managers, we should ask ourselves questions of practicality and uncertainty. As managers, we must continue to use the best available science, but we can't be ruled by science. Ultimately, we have to make policy decisions that incorporate other values. Both scientists and managers have a measure of responsibility, and with that, comes accountability.