CLIMATE WARMING, REDUCED SNOW, AND FREEZING INJURY COULD EXPLAIN THE DEMISE OF YELLOW-CEDAR IN SOUTHEAST ALASKA, USA

P. Hennon[1,2], D. D'Amore[1], D. Wittwer[2], A. Johnson[1], P. Schaberg[3], G. Hawley[4], C. Beier[5], S. Sink[5], G. Juday[5]

[1] USDA Forest Service, Pacific Northwest Research Station, Juneau, AK, USA
[2] USDA Forest Service, State and Private Forestry, Juneau, AK, USA
[3] USDA Forest Service, Northeast Research Station, Burlington, VT, USA
[4] University of Vermont, Burlington, VT, USA
[5] University of Alaska Fairbanks, Fairbanks, AK, USA
Email: phennon@fs.fed.us

ABSTRACT

Yellow-cedar (*Chamaecyparis nootkatensis*) is a valuable tree species that has been experiencing concentrated mortality known as yellow-cedar decline on 200,000 ha of largely pristine forests in Southeast Alaska. Mature trees that regenerated and grew during the Little Ice Age have been dying on low elevation sites with wet soils and open canopies for about 100 years. We propose the following hypothesis to explain tree death (methods in parentheses): landscape features (digital elevation model via LiDAR) and soil properties (soil descriptions) produce poor drainage (wells and piezometers) which create open canopy forests (LiDAR and hemispherical photography) and shallow rooting; exposure allows soils to warm in early spring (air and soil temperature loggers) which triggers dehardening, the loss of cold tolerance, and eventual spring freezing injury (electrolyte leakage testing of tissues). The distribution of yellow-cedar decline is associated with areas of low snowpack in winter and spring. Snow delays soil warming and presumably protects yellow-cedar roots through periods of spring frosts. Limited to higher elevations throughout most of its natural range, perhaps yellow-cedar migrated to lower elevations during the Little Ice Age, and these trees are now vulnerable to the lack of protective snow in these exposed, open canopy forests where forest decline is now severe.

427

INTRODUCTION

Yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach[1]), is a commercially, ecologically, and culturally important tree species in Alaska and British Columbia. The species has an extensive natural range from the California-Oregon border in forested montane areas to Prince William Sound in Alaska. It is limited to high elevation throughout most of its range, except in the northern portions, especially in Alaska where yellow-cedar grows from near timberline down to sea level (Harris, 1990). An extensive mortality problem (Fig. 1) known as yellow-cedar decline occurs on about 200,000 hectares in southeast Alaska (Wittwer et al., 2004) and a smaller amount in nearby British Columbia (Hennon et al., 2005) complicates the management of this valuable tree. This paper summarizes our current understanding of this ecological problem, with an emphasis on the leading hypothesis of the causal mechanism and the contributing role of climate. We discuss the historical distribution of the tree, how it may have responded to past fluctuations in climate, and provide a proposed management strategy for the species in the context of a warming climate.

Figure 1   Yellow-cedar decline on a pristine hillside just above sea level on Chichagof Island, southeast Alaska.

---

[1] Recently, there has been a proposal to move yellow-cedar to the genus *Callitropsis* (e.g., *Callitropsis nootkatensis* (D. Don) Örsted) based on its affinitiy with a newly discovered tree species in northern Vietnam (Little et al., 2004).

428

The Setting, Southeast Alaska

Southeast Alaska is a landscape of complex geologic origins (Conner and O'Haire, 1988) where accreted terrain and faults have created many islands and deep fjords that bisect the mountainous mainland.   The current climate of southeast Alaska is hyper-maritime, with abundant year-round precipitation and no prolonged dry periods.   The temperature regime is cryic, with high summer temperatures mediated by abundant cloud cover, and frequent low-intensity precipitation events. Winter temperatures average near freezing for the winter months at many weather stations, creating widely variable amounts of winter snow. Without fire as a disturbance factor, the region supports the largest temperate rainforest in the world, which extends south through British Columbia. The forests are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and smaller amounts of mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), shore pine (*Pinus contorta* Dougl.), and two cedars, western redcedar (*Thuja plicata* Donn) and yellow-cedar. Cool temperatures, short growing seasons, and saturated soils slow decomposition of dead plant material, resulting in peat formation. Slope and soil properties including peat accumulations, produce gradients of soil drainage that are largely responsible for driving forest productivity from large-stature, closed canopy forests on well drained soils to stunted, open canopy forests on saturated peat soils (Neiland, 1971).

HISTORICAL CLIMATE AND YELLOW-CEDAR PALEOBOTANY IN SOUTHEAST ALASKA

Fossil Record

The cypress family, Cupressaceae, evolved some 200,000 million years ago in the Triassic Period (Taylor and Taylor, 1993). Taxa with affinity to yellow-cedar first appeared in the Miocene (Kotyk et al. 2003), although similar macrofossil foliage dates back to the Eocene (Axelrod, 1976) and cones to the Late Cretaceous. The fossil record indicates that *Chamaecyparis* was more broadly distributed in the northern hemisphere than at present, but appears to have been, and continues to be, confined to moist climates, and some genera were extirpated with climate shifts to drier environments (Kotyk et al. 2003). Fossil assemblages from Vancouver Island in British Columbia reveal that species present in today's forests existed before the last glacial epoch (Hebda, 1996). Evidence of cedar before the last glacial maximum approximately 30,000-50,000 years ago was abundant in Oregon, but sparse in southeast Alaska and British Columbia (Hebda, 1996). The post-glacial migration of yellow-cedar to British Columbia may have been from this southern source, but the fossil evidence is not conclusive.

429

Pleistocene Refugia

The last glacial maximum in southeast Alaska extended until between 16,000 and 12,000 years BP, before which time southeast Alaska was thought to have been covered by ice (Hamilton, 1994). Several areas in coastal Alaska near Lituya Bay (Mann, 1983), Prince of Wales Island (Heaton et al., 1996), and to the south in the Queen Charlotte Islands of British Columbia (Warner et al., 1982), were considered to be unglaciated refugia, but many authors believed only tundra and high elevation species existed there during the glacial maximum. Mann and Hamilton (1995) assumed that tree species did not survive in the refugia in Alaska. Large areas in interior Alaska that were not glaciated may have served as refugia for plants, but most tree species were assumed to have recolonized southeast Alaska by migrating along the coast of British Columbia from non-glaciated regions to the south (Heusser, 1983). Recent discovery of human remains and bones of large predators in caves on Prince of Wales Island in Alaska (Dixon et al., 1998), as well the current distribution of several plants and animals, however, all indicate the existence of sizable low elevation refugia in the southwestern portion of Alaska's panhandle (Carrarra et al., 2003). Here, trees and other sub-alpine vegetation existed during the late Pleistocene and then provided epicenters for subsequent recolonization as glaciers receded.

Pollen Studies And Climate

Climate during the Holocene Epoch can be interpreted from the composition of trees and other plants from pollen profiles taken from lake and peat sediments, including 17 sites investigated by Heusser (1952, 1960). These pollen profiles provide direct evidence of the post-glacial abundance of conifers in the region.

Table 1   Interpretation of late Pleistocene and Holocene climate and dominant vegetation. Adapted from narrative in Viens, 2001

Years BP[1]	Climate[2]	Dominant vegetation
16,000 - 12,500	Cool dry	Tundra/shrubs
12,500 - 9,000	Warm, dry	Pine, alder, willow
9,000 - 6,800	Warm, wet	Spruce, hemlock
6,800 - 4,500	Trending wet, cool	Hemlock, spruce, cedar
4,500 − present	Cool, wet	Modern flora

[1] These are coarse time intervals and do not align precisely with many of early Heusser`s publications which were uncalibrated radio C-14 dating.

[2] Interpretation of climate, mainly from the occurrence of vegetation and knowledge about each species` ecological requirements, but also on peat accumulation.

Pollen analyses indicate shrub plant communities colonized the newly exposed terrain as glaciers began to retreat. Pollen profiles (e.g., Heusser, 1960) consistently reveal that pine woodlands with alder and willow dominated landscapes during a warm dry period, perhaps with cold winters, until about 9,000 years ago. Alder declined as spruce became more plentiful, probably the result of an abrupt change in climate that is interpreted to have been a milder, wetter climate (Peteet, 1986).

Western hemlock thrives in maritime climates without fire and is the most abundant tree species in today's forests of southeast Alaska. Western hemlock and mountain hemlock appeared in significant levels about 7,900 and 5,600 years ago, respectively, indicating cooler and wetter conditions. Peat accumulation also increased at this time, a suggestion that cooler and wetter climate was slowing decomposition rates. Temperatures and precipitation reached levels relatively similar to the current maritime climate about 4,500 years ago, both in Alaska (Heusser et al., 1985) and British Columbia (Mathewes and Heusser, 1981). This date corresponds to the establishment of modern western hemlock-Sitka spruce composition evident in many pollen cores (Viens, 2001).

Yellow-Cedar Historic Abundance

Unfortunately, yellow-cedar was not included in the early pollen studies because, as Heusser (1960) stated (Page 78), the pollen of *Chamaecyparis* and some other species had, "fragility and non resistance to decay….it was decided they be omitted [from analysis]." Another problem is that pollen of yellow-cedar is difficult to distinguish from western redcedar and juniper and is often lumped as "Cupressaceae pollen" or "cedar-type pollen." Cupressaceae was included in several more recent pollen studies in British Columbia just south of Alaska. Cupressaceae pollen became abundant about 7,000 years ago (Banner et al., 1983; Hebda and Mathewes, 1984), indicating a shift in climate there.

Both a cool wet climate, and associated soil development of organic material impeding drainage (Ugolini and Mann, 1979), favor both cedar species (Banner et al., 1983, Hebda 1983). Hebda (1983) reported that Cupressaceae pollen made a relatively recent appearance about 3,000 years ago in pollen profiles at a bog site on northern Vancouver Island in British Columbia. Also, Hebda stated that the pollen of western redcedar and yellow-cedar is under-represented in modern pollen profiles relative to surrounding forests and their pollen may not disperse as fully as other species. Species such as pine and alder are likely over-represented because of their copious pollen production. Mathewes (1973) detected the presence of western redcedar further south in British Columbia as early as 10,370 years ago, but found the species expanding about

6,600 years ago and then becoming dominant in only the last 3,000 years. New research in southeast Alaska includes the pollen of Cupressaceae and is revealing a similar pattern of the cedars becoming more prevalent about 5,000 years ago (Tom Ager, USGS, Pers. Comm.). Ager's research should shed more light on how long the cedars have been in Alaska and how their populations fluctuated, filling the knowledge gap for these species in the early pollen studies.

The late Holocene (4,500 years BP to 200 years BP) continued to be moist and cool and the cedars, including yellow-cedar, probably thrived and expanded their populations from various initial locations. Late in the Holocene record, there was a cooler shift, known as the "Little Ice Age", some 500 years ago. The influence of the so-called Little Ice Age on the climate of southeast Alaska is not clearly understood, but advances and retreats of glaciers appear to demonstrate an influence (Viens, 2001). The onset of yellow-cedar decline in the late 1800s (discussed below) roughly coincides with the end of the Little Ice Age. Information on the ages of canopy-level yellow-cedar trees (i.e., nearly all > 100 years old, (Hennon and Shaw, 1994)), suggests that the trees that died throughout the 1900s, and those that continue to die, regenerated and grew into their dominant positions during the Little Ice Age. We speculate that yellow-cedar colonized low elevation sites during this period, which probably had a more consistent winter and spring snowpack.

Yellow-Cedar Current Distribution In Southeast Alaska

For such a valuable tree species, the current distribution of yellow-cedar in southeast Alaska is not well known. Yellow-cedar reaches its greatest dominance in habitats near bogs, and other poorly drained sites, probably because of its inability to compete with western hemlock and Sitka spruce on better drained more productive sites (Neiland, 1971; Harris ,1990) Much of the mapping of plant communities in southeast Alaska is based on interpretation of aerial photographs where there are problems in visually distinguishing yellow-cedar from western hemlock. Therefore, we used field plot data from USFS Forest Inventory and Analysis (FIA) to construct a coarse presence/absence map of yellow-cedar by highlighting areas between plots, which were on a grid approximately three miles apart. The resulting map (Fig. 2), illustrates that yellow-cedar is well distributed in most of the region, except for the northeastern portion where it is rare. This map fits our own observations; yellow-cedar is curiously absent from many large areas, despite apparently abundant suitable habitat in the vicinity of bogs.
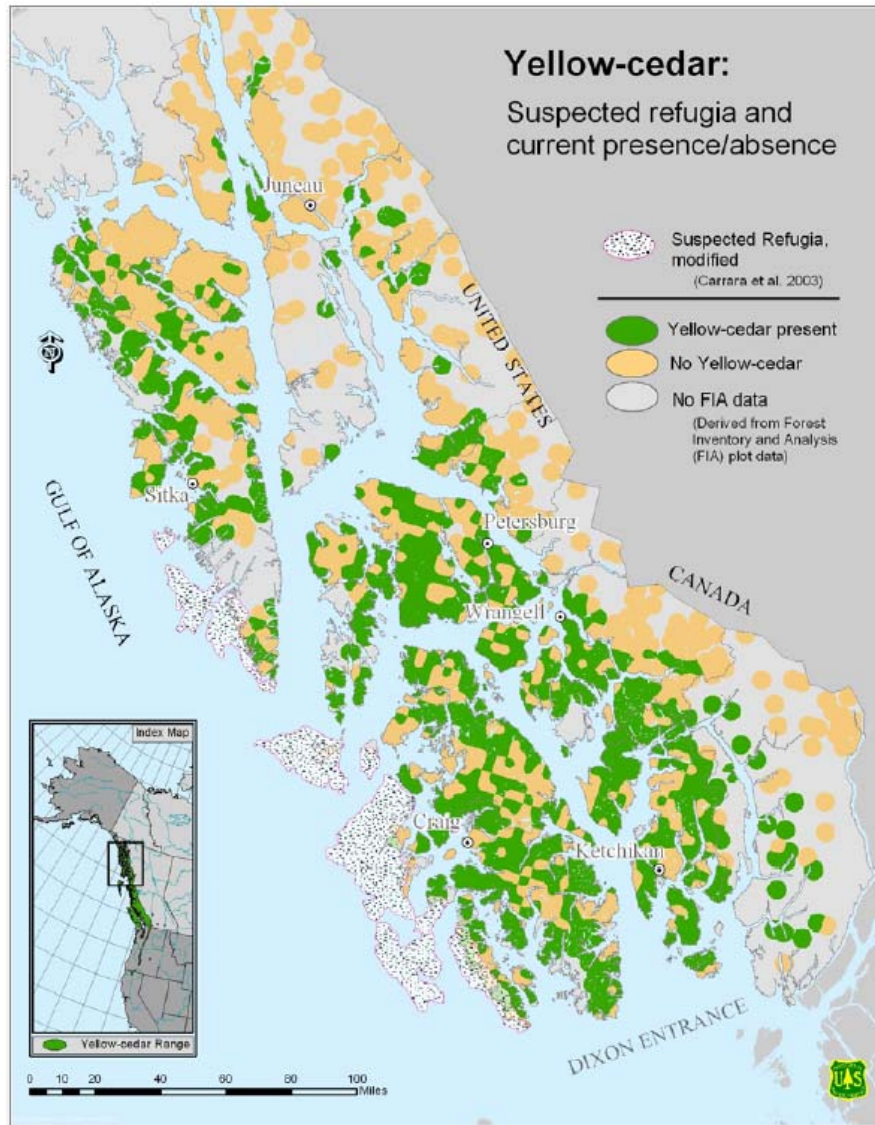
Figure 2   The occurrence of yellow-cedar (green) in southeast Alaska based on Forest Inventory and Analysis plot data. Also represented are areas of suspected refugia (Carrarra et al. 2003), which may represent seed sources for post-glacial migration and colonization.

We hypothesize that the rarity and absence of yellow-cedar in the

433

northeastern portion of the panhandle is due to distance from the suspected refugia (Carrarra et al., 2003) and the likelihood of a slow migration and colonization from the southwestern direction (Fig. 2). Yellow-cedar may have survived the Pleistocene in these refugia as a minor component of forests where it tolerated the harsher periods of the early Holocene by existing on favorable microsites such as seeps. Then about 6,600 years ago during favorable cool, wet periods it may have begun to expand its range. Hebda (1997) suggests a similar scenario in British Columbia; yellow-cedar could have survived unfavorable times as a shrubby form in British Columbia refugia on western portions of Vancouver and Queen Charlotte Islands. A preliminary evaluation of the genetic structure of the species throughout its natural range (Ritland et al. 2001) found that yellow-cedar in southeast Alaska is genetically distinct from populations in British Columbia and further south, supporting the scenario that populations of yellow-cedar in southeast Alaska originated in Alaskan refugia. Interestingly, a disjunct Prince William Sound population (Hennon and Trummer, 2001) to the northwest had affinity with populations in the Queen Charlotte Islands and may have origins there (Ritland et al., 2001).

This very slow post-glacial migration from refugia in the southwestern parts of the panhandle may be explained by the poor regeneration trait of yellow-cedar (Harris, 1990, Klinka, 1996). The species has small cones that require two years to develop, does not produce much seed, and seed does not reliably germinate (Pawuk, 1983). In the 5,000 to 6,000 years since the climate and habitat may have been suitable, yellow-cedar is apparently still actively migrating and colonizing new habitat to the northeast. We are now initiating a field dendrochronology study of several small populations of the species near Juneau in an attempt to determine if any of these are newly established populations. Our map of the current yellow-cedar distribution in southeast Alaska (Fig. 2) could be the basis for a genetics study to map similarities among populations regionally to evaluate the refugia-slow migration pathway hypothesis.

Yellow-Cedar Dendrochronology

Laroque and Smith (1999) produced the first published tree ring analysis of yellow-cedar. They evaluated growth patterns of yellow-cedar back to 1800 growing on high elevations sites on Vancouver Island, British Columbia. Six different temperature and precipitation factors were associated with ring width variation. There is only one other published chronology of tree growth in southeast Alaska; Viens (2001) established a 450 year chronology for mountain hemlock growing at timberline near Petersburg, Alaska. The mountain hemlock chronology may prove useful in comparing the growth of yellow-cedar in and away from declining forests. In an effort to fill the dendrochronological gap in

434

southeast Alaska, two new research efforts based out of University of Alaska, Fairbanks have been initiated to provide robust sampling of living yellow-cedar trees over a range of sites, including different elevations and varying levels of forest decline. One goal is to produce a growth chronology for yellow-cedar and associate it with climate data from weather stations through the 1900s. The other goal is to detect episodes of injury, or poor growth, that can be associated with weather scenarios that align with the leading hypothesis described below.

EARLY RESEARCH ON CEDAR DECLINE

Research on yellow-cedar decline outlined below began in the 1980s and was focused on evaluating biotic factors that were suspected as the primary cause of yellow-cedar decline. Also, the timing of death for yellow-cedar trees was coupled with ground surveys to determine when the problem may have been initiated and to establish patterns of subsequent spread.

Symptomology And Biotic Factors

Dying trees were examined for symptoms in their roots, bole, and crown (Hennon et al., 1990). A sequence of symptoms was developed whereby fine root death was the earliest symptom of tree death, followed by death of small diameter roots, necrotic lesions on coarse roots, and finally necrotic lesions spreading from dead roots vertically from the root collar up the side of the bole. Crown symptoms followed the early root symptoms and crowns generally died as a unit with proximal foliage dying first, then as trees finally died, distal foliage died. Generally, the study of symptoms suggested a below-ground problem for affected trees. The following groups of organisms were evaluated as potential pathogens involved in the decline syndrome, but each was ruled out by inoculation studies or by the lack of association with symptomatic tissue or dying areas of the forest.

Higher fungi (Hennon, 1990; Hennon et al.; 1990)

Oomycetes (Hansen et al., 1988; Hamm et al.; 1988)

Insects (Shaw et al., 1985)
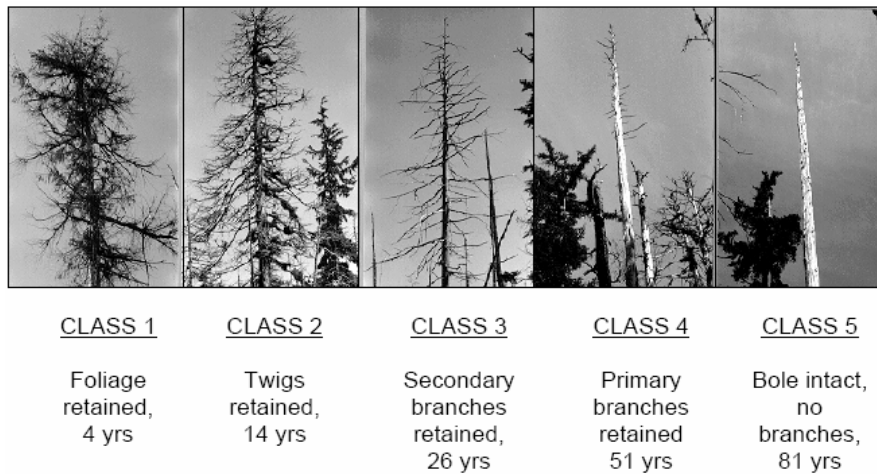
Nematodes (Hennon et al., 1986)

Viruses and mycoplasmas (Hennon and McWilliams, 1999)

Bears (Hennon et al., 1990)

The general conclusion from these evaluations of symptoms and possible biotic factors was that no contagious organism was the primary cause of the decline problem (Hennon et al., 1990; Hennon and Shaw, 1997).

Epidemiology

A snag classification (Fig. 3) with associated time-since-death estimates (Hennon et al., 1990) was developed and used in ground surveys (Hennon et al., 1990) to reconstruct changes in populations through the 1900s. The remarkable decay resistant heartwood of dead yellow-cedar trees (Kelsey et al., 2005) allows them to remain standing for 80 to 100 years after death, making this reconstruction possible. The onset of yellow-cedar decline occurred in about 1880 to 1900 on most of the sites where trees are still dying. Thus the decline is progressive in declining forests, which now contain long-dead trees, more recently-killed trees, dying trees, and some survivors, usually other tree species (Hennon and Shaw, 1997). The mortality problem is typically associated with wet, poorly drained soils with long-dead cedars often on the wettest soils. Recently-killed and dying trees are frequently found on better-drained soils and on the perimeters of the dying forests, indicating a slow spreading pattern along a hydrology gradient (Hennon et al., 1990). These strong relationships with site factors, particularly hydrology, were another indication that the primary problem was not strictly biotic in nature.

| CLASS 1	CLASS 2	CLASS 3	CLASS 4	CLASS 5
Foliage retained, 4 yrs	Twigs retained, 14 yrs	Secondary branches retained, 26 yrs	Primary branches retained 51 yrs	Bole intact, no branches, 81 yrs

Figure 3 Yellow-cedar snag classification with estimates of time-since-death (Hennon et al. 1990)

YELLOW-CEDAR DECLINE MAPPING AT THREE SPATIAL SCALES

Along with reconstructing mortality through the 1900s on the temporal scale discussed above, we are evaluating the yellow-cedar problem at three spatial scales: broad scale ($\sim$7x10^6 km^2, southeast Alaska), mid-scale ($\sim$800 km^2; e.g,

medium-sized island), and fine scale (~1km^2; small watershed). Each spatial scale provides unique clues about the cause of yellow-cedar decline, and will also be highlighted in the development of a management strategy for the species.
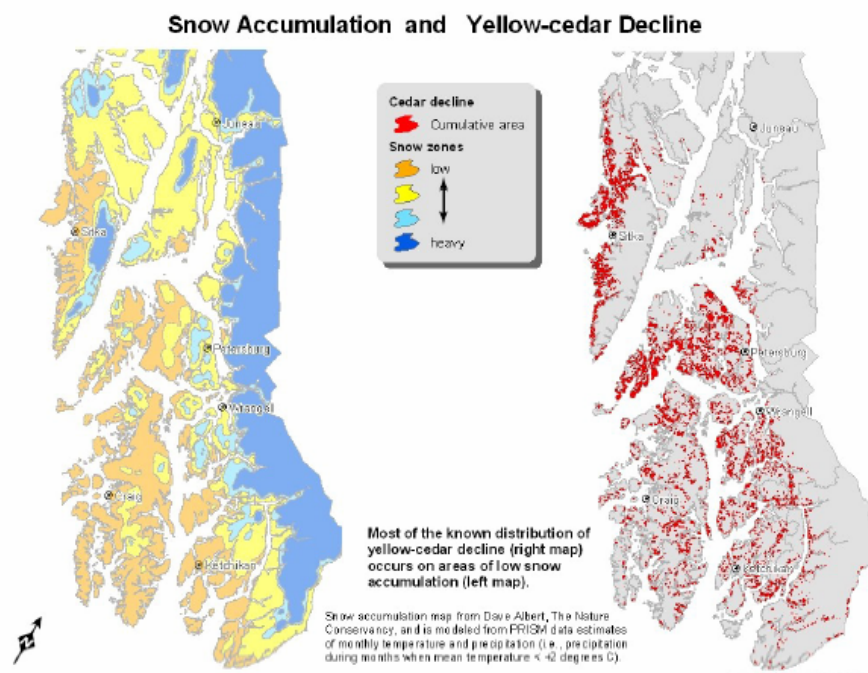
Figure 4 Map depicting snow levels (left) and the occurrence of yellow-cedar decline (right). Note the close association of decline with the lowest snow zone. Snow zone map developed by Dave Albert of the Nature Conservancy using PRISM data estimates of temperature and precipitation. Cedar decline map based on USFS aerial survey.

Broad Scale

For the broadest scale, we developed a distribution map that depicts more than 2,500 locations totaling over 200,000 hectares of dead and dying yellow-cedar forests (Wittwer, 2004) (Fig 4). This map was derived from sketch mapping from small aircraft, an approach that yields inexact locations and polygon boundaries. However, it is instructive to examine broad areas where decline is present or absent and relate any pattern to regional variation in climate. In an early use of the map, we found the forest decline to align with the warm side of average winter temperature isotherms (Hennon and Shaw, 1994), an early suggestion that climate was involved in the problem. Here, we compare the distribution of yellow-cedar decline to the first detailed model of snow

437

accumulation zones in southeast Alaska (Fig. 4). The snow accumulation model was developed courtesy of Dave Albert of the Nature Conservancy, and is derived from PRISM data estimates of monthly temperature and precipitation (i.e., precipitation during months when mean temperature <+2ºC). Note that close association between occurrence of yellow-cedar decline and the lowest snow zone.

Our distribution map captures the occurrence of yellow-cedar mortality in Alaska, but not in adjacent British Columbia. Recently, we detected intensive areas of yellow-cedar decline about 150 km south into British Columbia where it often occurred at about 300 to 400 m elevation (Hennon et al., 2005). Surveys by the British Columbia Forest Service continue in an attempt to map the southern extent of the problem.

Mid Scale

We produced a higher resolution mid scale map of an area of Baranof and Chichagof Islands (~800km^2) by delineating polygons of yellow-cedar decline on color infrared photographs rather than by aerial sketch mapping. We use this higher resolution map to evaluate the association of the decline problem with landscape position features including slope, aspect, and elevation. Our mapped polygons of yellow-cedar decline in this study area are concentrated at lower elevations: higher amounts below 150m, lesser amounts between 150 and 300m, and very little above 300m. Yellow-cedar decline occurs on all aspects within these zones, but more decline was mapped on warm aspects (south and southwest). Currently, we are expanding this work to Mount Edgecumbe, an extinct volcano near Sitka that has radial symmetry and a fairly even slope supporting open canopy forests that extend to nearly timberline. These features help control confounding factors and allow us to detect the direct influence of elevation and aspect on snow and the decline problem.

Fine Scale

Research at the small watershed scale is directed at an understanding of how forest conditions vary over local areas of a landscape. We established vegetation plots on 100m grids at two small watersheds, Goose Cove on Baranof Island and Poison Cove on Chichagof Island, to measure live and dead trees and environmental variables (D'Amore and Hennon, 2006). Also, we used low altitude color infrared photographs to produce a forest classification based on canopy cover and the extent of tree death, resulting in four zones: bog, scrub, productive dead, and productive live. The hydrologic, soil, and temperature factors described below were then compared among these zones, as well as correlated with degree of tree death (expressed as percent basal area dead).
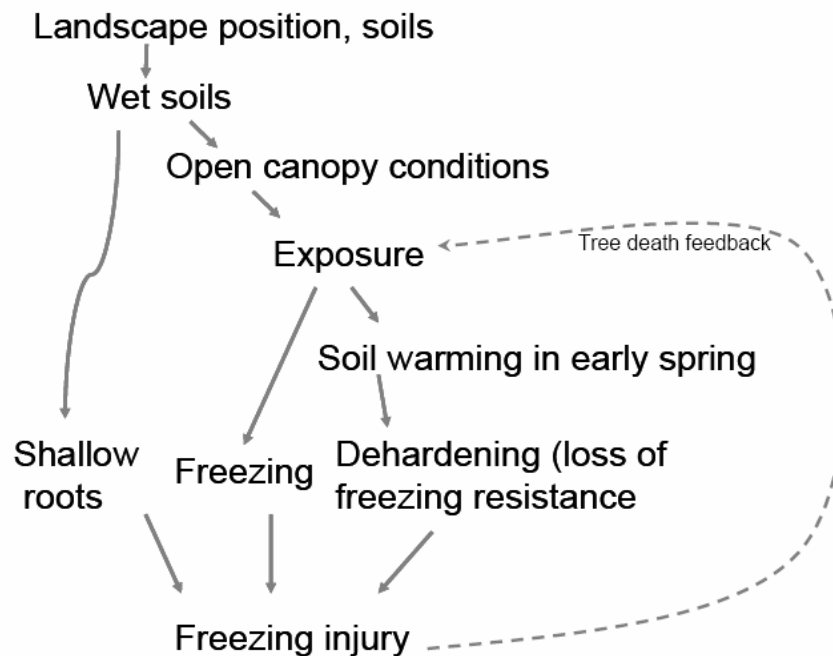
438

Figure 5 Hypothetical cause of yellow-cedar decline.

ABIOTIC FACTORS AND EVALUATING A LEADING HYPOTHESIS

Abiotic Risk Factors

We evaluated the leading abiotic factors potentially associated with yellow-cedar decline (D'Amore and Hennon, 2006) and provide a summary here. Soil saturation was associated with dead trees, particularly in the central patches of decline. The soil saturation-dead tree relationship was not consistent, however, as some areas of decline occurred on well drained soils, and saturated bogs sites at a higher elevation had little cedar tree death. Soil chemistry was examined, with a focus on aluminum, calcium, and acidity and their correlation with tree death. Aluminum toxicity (Lawrence et al., 1995; Lawrence et al., 1997) or low acidity (Klinger, 1990) could potentially reach levels that would damage roots as soils become saturated, but no relationship of either factor with dead trees was found. Depleted soil calcium is known to be involved in the cold tolerance of forest trees (Schaberg et al., 2001; Schaberg et al., 2002). Rather than occurring at low levels indicating susceptibility to freezing, soil calcium was found in high concentrations where yellow-cedar trees had died, probably because of enrichment from the senescence and decomposition of cedar tissues. Soil and air temperatures

439

emerged as the abiotic factors most highly correlated with the death in the cedar forests (see below). Thus, this study and the collective research that preceded it were the foundation for a new hypothesis that we elevated to explain yellow-cedar decline (Fig 5). Each interaction in this complex hypothesis is explained below.

Landscape Position, Soil Properties Create Wet Soils

The association of yellow-cedar decline with bog plant communities can be seen from aircraft or on aerial photography. Dead trees frequently occur around the edges of bogs, or on hillsides with mosaics of bogs and forests supported by moderate drainage (Hennon et al., 1990). The yellow-cedar mortality problem is not known to occur where yellow-cedar grows with western hemlock in productive forests that are not in proximity to bogs. Johnson and Wilcock (2002) were the first to measure hydrology directly on decline sites, and found that dying portions of forests had larger hydrologic contributing areas and remain saturated longer than surrounding healthy forests. Sampling in two watersheds, D'Amore and Hennon (2006) reported higher water table levels in some portions of declining forests, but not where recent mortality had occurred near the perimeter of dead and dying trees indicating that the mortality occurs across several soil drainage classes.

Wet Soils Govern Canopy Cover

Soil drainage drives the stature and productivity of forests in southeast Alaska, which in turn controls canopy cover. Saturated soils lead to scattered stunted trees that produce almost no cover (e.g., on bogs), for example. Regardless of tree death, overall tree productivity was highly correlated with mean water table values measured in wells at our study sites (D'Amore and Hennon 2006). Currently, we are using LiDAR-derived digital elevation models (resolution is sub-meter) of the ground surfaces to map drainage patterns relative to tree death and canopy cover.

Open Canopy Conditions Influences Exposure

We are using two methods to evaluate canopy cover and exposure at two watersheds: hemispherical (i.e., "fisheye") photographs and LiDAR canopy interception. Results on canopy cover from these bottom-up and top-down views are highly correlated. LiDAR measures have the advantage of modeling canopy cover across the entire watershed, rather than rely on separate locations where hemispherical photographs are taken. Our tree plot information is providing values of both live and dead trees to compare to these two measures of canopy cover. Canopy cover is largely driven by measures of live trees (e.g., basal area

440

values driven by hydrology), but dead trees also make a smaller, and significant contribution. These evaluations suggest that exposure (i.e., open canopy conditions) was controlled by hydrology through the suppression of forest productivity by wet soils in the initial phases of yellow-cedar decline. These wet areas are occupied by the oldest snags that died decades ago (D'Amore and Hennon, 2006). The exposed, open canopy condition has developed more recently at the perimeters of decline patches on soils with better drainage, through a feedback of tree death itself.

Exposure Affects Dehardening And Freezing Temperatures

Soil temperature and air temperature near the ground are primarily controlled by canopy cover (D'Amore and Hennon, 2006). Sites with less canopy cover have greater daily maxima, lower daily minima, and greater daily ranges of air temperature. The accumulation of soil temperature, expressed as soil degree days, is greater in areas of less canopy cover. These influences of canopy cover on air and soil temperature fluctuations are most pronounced in spring. We are continuing to associate air and soil temperature with canopy cover values derived from hemispherical photography and LiDAR canopy modeling (described above).

Temperature appears to have a particularly strong influence on the fall hardening and spring dehardening processes for yellow-cedar (Puttonen and Arnott, 1994; Hawkins et al., 2001). Thus, we propose that yellow-cedar trees growing in microsites with less canopy cover, controlled by either hydrology or mortality feedback, are triggered to deharden prematurely by warming in late winter and early spring.

Dehardening, Shallow Roots, and Freezing Cause Tree Death

We evaluated the seasonal cold tolerance of yellow-cedar and co-existing western hemlock in open- and closed-canopy forests and at several elevations at one of our study sites (Schaberg et al., 2005). In fall, yellow-cedar in open canopy settings achieved deeper dehardening than cedar in closed-canopy, but western hemlock appeared unresponsive to canopy conditions, instead relying primarily on photoperiod. In winter, yellow-cedar had cold tolerance to about -40C, colder than any recorded temperature for the region. Susceptibility of yellow-cedar to cold temperatures develops in later winter and spring. In our testing of tree tissues (Schaberg et al., 2005), yellow-cedar dehardened almost 13C more than western hemlock. Also, trees that we tested growing above 130m elevation were more cold hardy than those growing below 130m.

We have observed severe freezing injury to yellow-cedar seedlings growing in Juneau across several years, each time at the end of March or early

441

April. Based on these observations and our cold tolerance testing of mature trees, we initiated a study on seedlings to more intensively evaluate the dehardening and cold tolerance of root and foliage tissue in late winter and early spring. Results should help us understand which tissues are at greatest risk of freezing and to what degree soil warming initiates dehardening. This line of research on cold tolerance and freezing injury is the most direct approach of evaluating the primary cause of yellow-cedar decline.

Protection Of Snow

Snow appears to protect yellow-cedar from this presumed freezing injury. Our measurements of snowpack at the Poison Cove study site indicate that yellow-cedar growing around an open-canopy bog at 150m, a setting without the decline problem, has snowpack through April or May during some years. Snow appears to offer some form of protection for yellow-cedar, perhaps by either 1) delaying the dehardening process, or 2) protecting fine shallow roots from freezing. In either case, the presence of snow through March and April apparently allows yellow-cedar to pass a period of potential vulnerability that affects trees growing without snow. At our mid-scale analysis, the lack of spring snow may explain why yellow-cedar decline is limited to lower elevations and why it reaches higher elevations on warm aspects compared to cold aspects. At the broad scale, the distribution of yellow-cedar decline aligns very closely with the lowest snow zone (Fig. 4). Some change in the environment must have initiated yellow-cedar decline. It is possible that reduced late winter and spring snowpack as the climate emerged from the Little Ice Age represents that environmental trigger.

YELLOW-CEDAR MANAGEMENT

Wood Properties Of Dead Trees

The desirable wood characteristics of yellow-cedar put great pressure on the resource of this species for timber production. The large acreage of yellow-cedar decline, coupled with the value of wood from dead trees (see below), suggests salvage opportunities. Before salvage recovery could proceed, information was needed on how the characteristics of wood from dead trees compared to that of live trees. Thus, several years ago, we initiated a series of studies to evaluate the value of wood from dead yellow-cedar. Each of the studies below employed the same snag classification (Fig. 3) system for trees dead up to 100 years that was developed for epidemiological studies (Hennon et al., 1990). It provided time-since-death estimates for dead standing yellow-cedar trees in five recognizable stages of deterioration; the oldest class 5 snags are standing with no limbs or sapwood and died an average of 81 years ago. Using this classification

442

system allowed us to determine changes in tree and wood properties through time, and also to integrate results among studies.

> Pattern of tissue deterioration (e.g., bark, sapwood) (Hennon et al., 2000)
>
> Recovery of wood volume (Hennon et al., 2000)
>
> Recovery of wood grade (Hennon et al., 2000)
>
> Strength properties (McDonald et al., 1997; Green et al., 2002)
>
> Durability/decay resistance (DeGroot et al., 2000)
>
> Heartwood chemistry (Kelsey et al., 2005)

The unique heartwood chemistry of yellow-cedar greatly limits decay in standing dead yellow-cedars. All wood properties are preserved for the first 26 years after tree death. The first change in a wood property then occurs when the heartwood chemistry begins to change (Kelsey et al., 2005). Decay resistance is reduced somewhat in the older two snag classes (DeGroot et al., 2000), as are minor reductions in wood grade and the volume of wood recovered at a mill (Hennon et al. 2000). Remarkably, strength properties are not measurably different compared to wood from live trees, even 81 years after death. The preservation of wood properties decades after death, coupled with the large acreage of yellow-cedar decline, suggest promising salvage opportunities to meet the demands of producing yellow-cedar wood.

Yellow-Cedar Regeneration

Yellow-cedar does not reproduce prolifically (Harris, 1990; Klinka, 1996) and may require measures to ensure that it successfully regenerates. Vegetation reproduction through layering (i.e., rooting of lower branches) occurs, but this phenomenon is restricted to open bog sites where live lower limbs contact the ground (Hennon et al., 1990). The degree to which seed tree harvests promote yellow-cedar regeneration is unknown in Alaska. A planting trial established in 1986 of yellow-cedar seedlings demonstrated that the species can be regenerated on logged sites, as long as it is planted quickly after harvest (Hennon, 1992) (Fig. 6). Barriers to artificial regeneration through planting are mainly 1) competing vegetation, 2) deer browse, and 3) spring freezing injury. Research and development are needed on each of these topics related to the early establishment phase of regeneration. Once established, thinning can be used to favor yellow-cedar to maintain its competitive status with other conifers. Silvicultural experience with yellow-cedar is needed in the region to ensure that the species can be managed long term to produce timber and other resource needs. A genetics

program aimed at breeding for slow spring dehardening and freezing resistance could be employed to restore yellow-cedar in future managed forests.

Figure 6 Yellow-cedar 18 years after planting on a non-decline site that was logged and burned at Anita Bay, Etolin Island, Southeast Alaska (Hennon, 1992). Burning or scarification may be necessary to promote yellow-cedar in its competition with western hemlock and shrubs.

444

Synthesis And Suggested Yellow-Cedar Conservation Strategy

We propose a management strategy that shifts more of the timber production to the dead yellow-cedar forests, and active regeneration of the species on sites not currently declining. The various wood properties are preserved by the unique heartwood chemistry for decades, only diminishing slightly in the oldest snag classes some 50 and 80 years after tree death. Evaluating the habitat potential of dead standing yellow-cedar trees for birds and small mammals is still a research need. Information on tissue deterioration through time, and the persistence of hard wood in snags (Hennon et al., 2002), might suggest that minimal use of yellow-cedar snags would be found, however. Knowledge on the successional trajectory in the declining yellow-cedar forests is also needed. Other conifer species, already present as understory trees, appear to be favored where the yellow-cedar overstory has died. This successional process will likely play out whether or not declining forests are salvaged.

To compensate for losses due yellow-cedar decline, and yellow-cedar removed by commercial logging on other sites, an active forest regeneration program is needed. The success of natural regeneration (e.g., seed tree harvests) needs to be evaluated. Yellow-cedar can be successfully regenerated by planting either seedlings (Hennon, 1992) or rooted cuttings (Russell, 1993), but the barriers to seedling performance (competing vegetation, deer browsing, and spring freezing) need to be considered. Favoring yellow-cedar during thinning operations can increase the yellow-cedar component in managed forests; however, planting may be necessary to establish a viable population to be manipulated.

Knowledge about the current and future distribution of yellow-cedar decline would aid forest managers in decisions about where to perform salvage operations and where to actively regenerate and promote yellow-cedar. The current distribution of decline is known and available as a GIS layer (Wittwer, 2004). Managing this long-lived tree species will require predicting where the decline problem will occur in the next few centuries, however. Thus, a clear understanding of the mechanism of decline, future climate projections, and landscape modeling will be needed to solve the problem of where to favor the species in the future. Our current knowledge suggests that yellow-cedar should be favored in:

1) northern and eastern regions of southeast Alaska that have cold winters,

2) higher elevations within the distribution of yellow-cedar decline, and

3) better drained soils supporting greater forest productivity where roots penetrate more deeply and shade cools soils during early spring.

445

SUMMARY

An explanation of the cause of yellow-cedar decline must account for some particular vulnerability in this defense tree species and some change in the environment. Yellow-cedar appears to be susceptible to premature dehardening and spring freezing injury. Minor climate warming at the end of the Little Ice Age may have reduced late winter and spring snowpack, eliminating the protection offered by snow to this species which is adapted to higher elevations. If our explanation for yellow-cedar decline is correct, then this phenomenon represents an excellent example of how a shifting climate can cause dramatic changes in an ecosystem. The early historical onset and pristine environmental conditions in declining forests suggest that yellow-cedar decline is largely a natural process. The elusiveness of determining the cause of tree death and the complexity of our hypothetical scenario illustrate the difficulty in predicting ecosystem effects of climate change. After more than 20 years of research, the causal mechanisms and possible role of climate are just now coming into clarity. A more thorough understanding of the cause of yellow-cedar decline and the contributing role of climate will be necessary to manage this valuable tree species in the future.

REFERENCES

Axelrod, D.J., History of the coniferous forests, California and Nevada, *Univ. Calif. Publ. Bot.*, **70**, 1-62 (1976).

Banner, A., J. Pojar, and G.E. Rouse, Postglacial paleoecologoy and successional relationships of a bog woodland near Prince Rupert, British Columbia. *Can. J. For. Res.* **13**, 938-947 (1983).

Carrarra, P.E., T.A. Ager, J.F. Baichtal, and D.P. VanSistine, Map of glacial limits and possible refugia in the southern Alexander Archipelago, Alaska, during the late Wisconsin Glaciation, *Miscellaneous Field Studies Map*, MF-2424. US Geological Service, Denver, CO (2003)

Conner, C., and D. O'Haire. Roadside geology of Alaska, Mountain Press Publishing Co., Missoula, MT (1988).

Dixon, E.J., T.H. Heaton, T.E. Fifield, T.D. Hamilton, D.E. Putnam, and F. Grady, Late quaternary regional geoarchaeology of southeast Alaska karst: a progress report, *Geoarchaeology,* **12**, 689-712 (1998).

D'Amore, D.D., and P.E. Hennon, Evaluation of soil saturation, soil chemistry, and early spring soil and air temperatures as risk factors in yellow-cedar decline, *Global Change Biology*, **12**, 524-545 (2006).

Davradou, M., and B.J. Hawkins, Effects of plantation location and population on the seasonal freezing tolerance of yellow-cedar (*Chamaecyparis nootkatensis*) stecklings. *New For.,* **15**, 77-87 (1998).

DeGroot, R.C., B. Woodward, P.E. Hennon, Natural decay resistance of heartwood from dead,

standing yellow-cedar trees: laboratory evaluations, *For. Prod. J*., **50**, 53-59 (2000).

Green, D.W., McDonald, K.A., Hennon, P.E., J.W. Evans, J.W., and J.H Stevens, 2002. Flexural properties of salvaged dead yellow-cedar from southeast Alaska, *For. Prod. J*. **52**, 81-88 (2002).

Hamilton, T.D. Late Cenozoic glaciation of Alaska, Pp. 813-844, In, Plafker, G. and H. C. Berg (Eds.), Geology of North America, Geological Society of America, Boulder, CO (1994).

Hamm, P.B., E.M. Hansen, P.E. Hennon, and C.G. Shaw III, Pythium species from forest and muskeg areas of southeast Alaska, *Trans. Brit. Mycol. Soc.*, **91**, 385-388 (1988).

Hansen, E.M., P.B. Hamm, P.E. Hennon, and C.G. Shaw III, *Phytophthora drechsleri* in remote areas of southeast Alaska. *Trans. Brit. Mycol. Soc.*, **91**, 379-388 (1988).

Harris, A.S., *Chamaecyparis nootkatensis* (D. Don) Spach: Alaska-cedar, *In* Silvics of North America, Volume 1: Conifers, Agric. Handb. 654, U.S. Department of Agriculture, Forest Service, Washington, DC., Pp. 97-102 (1990).

Havranek, W.M., and W. Tranquillini, Physiological processes during winter dormancy and their ecological significance, Pp. 95-124, In Ecophysiology of coniferous forests. *Edited* by W.K. Smith and T.M. Hinckley. Academic Press, New York (1995).

Hawkins, B.J., J. Russell, and R. Shortt, Effect of population, environment, and maturation on the frost hardiness of yellow-cedar (*Chamaecyparis nootkatensis*), *Can. J. For. Res.,* **24**, 945-953 (1994).

Hawkins, B.J., J.H. Russell, and J. Arnott,. Cold hardiness of yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach), Pp. 531-554, In Conifer cold hardiness. F.J. Bigras and S.J. Colombo (Eds.), Kluwer Academic Publishers, Dordrecht, Netherlands (2001).

Heaton, T.H., S.L. Talbot, and G.F. Shields, An ice age refugium for large mammals in the Alexander Archipelago, Southern Alaska. *Quaternary Research,* **46**, 186-192 (1996).

Hebda, R.J., Late-glacial and post glacial vegetation history at Bear Cove Bog, northeast Vancouver Island, British Columbia, *Can. J. Bot*., **61**, 3172-3192 (1983).

Hebda, R.J., History of cedars in western North America. Pp. 5-13, In: Wiggins, G.G. (Ed.), Proceedings of the cedar symposium, May 28-30, 1996, Canada-British Columbia South Moresby Forest Replacement Account, Queen Charlotte City, BC (1996).

Hebda, R.J., Late Quaternary paleoecology of Brooks Peninsula. The Brooks Peninsula: an ice age refuge on Vancouver Island. In, R.J. Hebda and J.C. Haggerarty (Eds.), B.C. Parks, Victoria, B.C, *Occasional Paper* (1997).

Hebda, R.J. and R.W. Mathewes,. Holocen history of cedar and native cultures on the North American Pacific Coast. *Science* **225,** 711-3 (1984).

Hennon, P.E., Fungi on *Chamaecyparis nootkatensis, Mycologia*, **82**, 59-66 (1990).

Hennon, P.E., Survival and growth of planted Alaska-cedar seedlings in southeast Alaska, *Tree Planters' Notes*, **43**(3), 60-66 (1992).

Hennon, P.E., and C.G. Shaw III, Did climatic warming trigger the onset and development of yellow-cedar decline in southeast Alaska? *Europ. J. For. Path*., **24**, 399-418 (1994).

Hennon, P.E., and C.G. Shaw III, The enigma of yellow-cedar decline: what is killing these long-lived, defensive trees? *J. For.*, **95**, 12, 4-10 (1997).

Hennon, P.E.; C.G. Shaw III, and E.M. Hansen, Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska, *Forest Science*, **36,** 502-515 (1990).

Hennon, P.E., C.G. Shaw III, and E.M. Hansen, Symptoms and fungal associations of declining *Chamaecyparis nootkatensis* in southeast Alaska, *Plant Disease*, **74**, 267-273 (1990).

Hennon, P.E., D. D'Amore, S. Zeglen, and M. Grainger, Yellow-cedar decline in the North Coast District of British Columbia. Res. Note RN-549, Portland, OR, U.S. Dep. Agric., For. Serv., Pac. Northwest Res. Sta, 16p. (2005).

Hennon, P.E.; E.M. Hansen, and C.G. Shaw III, Causes of basal scars on *Chamaecyparis nootkatensis* in southeast Alaska, Northwest Sci., 64, 45-54 (1990).

Hennon, P.E., E.M. Hansen, and C.G. Shaw, III, Dynamics of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska, *Can. J. Bot.*, **68**, 651-662 (1990).

Hennon, P.E., G.B. Newcomb, C.G. Shaw III, and E.M. Hansen, Nematodes associated with dying *Chamaecyparis nootkatensis* in Southeastern Alaska, Plant Dis., **70**, 352 (1986).

Hennon, P.E., D.T. Wittwer, J. Stevens, K. Kilborn, Pattern of deterioration and recovery of wood from dead yellow-cedar in southeast Alaska, *West. J. Appl. For.*, **15**, 49-58 (2000).

Hennon, P.E., and L.M. Trummer, Yellow-cedar (*Chamaecyparis nootkatensis*) at the northwest limits of its range in Prince William Sound, Alaska, *Northwest Science*, **75**, 61-72 (2001).

Hennon, P.E., M.H. McClellan, P. Palkovic, Comparing deterioration and ecosystem function of decay-resistant and decay-susceptible species of dead trees, Pp. 435-444, In: Laudenslayer, W.F.; Shea, P.; Valentine, B.E. and others, (eds.), *Proceedings of the symposium on the ecology and management of dead wood in western forests, Nov. 2-4, 1999; Reno, NV*, USDA Forest Service General Technical Report PSW-GTR-181 (2002).

Hennon, P.E, and M.G. McWilliams, Decline symptoms do not develop with grafting from dying yellow-cedar, *Can. J. For. Res.,* **29**, 1985-1988 (1999).

Heusser, C. J. Late Pleistocene environments of North Pacific North America, *American Geographical Society Special Publication* **35** (1960).

Heusser, C.J. Pollen Profiles from southeastern Alaska, *Ecological Monographs*, **22**, 331-352 (1952).

Heusser, C. J. Vegetational history of the northwest United States, including Alaska. In Porter, S.C. (Ed.), Late Quaternary environments of the United States, Pp. 239-258, Minnesota Press, Minneapolis (1983).

Heusser, C. J., L.E. Heusser, and D.M. Peteet, Late-Quaternary climatic change on the American North Pacific coast, *Nature* **315,** 485-487 (1985).

Johnson, A.C. and P. Wilcock, Association between cedar decline and hillslope stability in mountainous regions of southeast Alaska, *Geomorphology*, **46**, 129-142 (2002).

Kelsey, R.G., P.E. Hennon, M. Huso, and J.J. Karchesy, Changes in heartwood chemistry of dead yellow-cedar trees that remain standing for 80 years or more in Southeast Alaska. *Journal of Chemical Ecology*, **31**, 2653-2670 (2005).

Klinger, L.F., Global patterns in community succession, 1. Bryophytes and forest decline, *Memoirs of the Torrey Botanical Club*, **24,** 1-50 (1990).

Klinka, K., Update on silvics of western redcedar and yellow-cedar, Pp. 14-28, In: Wiggins,

G.G. (Ed.), *Proceedings of the cedar symposium, May 28-30, 1996, Canada-British Columbia South Moresby Forest Replacement Account*, Queen Charlotte City, BC (1996).

Kotyk, M.E.A., J.F. Basinger, and E.E. McIver, Early Tertiary *Chamaecyparis* Spach from Axel Heiberg island, Canadian high arctic, *Canadian Journal of Botany* **81,** 113-130 (2003).

Laroque, C.P., and D.J. Smith, Tree ring analysis of yellow-cedar (Chamaecyparis nootkatensis) on Vancouver Island, British Columbia, *Can. J. For. Res.*, **29**, 115-123 (1999).

Lawrence, G. B.; David, M.B.; Shortle, W.C., Aluminum mobilization as a mechanism for calcium depletion in organic forest soil horizons. *Nature* **378**,162-165 (1995)

Lawrence, G. B.; David, M.B.; Shortle, W.C., Assessment of soil calcium status in red spruce forests in the northeastern United States. *Biogeochemistry* **38**,19-39 (1997).

Little, D.P., A.E. Schwarzbach, R.P. Adams, and C.F. Hsieh, The circumscription and phylogenetic relationship of *Callitropsis* and the newly described *Xanthocyparis* (Cupressaceae). *Amer. J. Bot.*, **91**, 1872-1881 (2004).

Mann, D.H., *The Quaternary history of the Lituya glacial refugium, Alaska,* Ph.D. thesis, University of Washington (1983).

Mann, D. H., and T.D. Hamilton, Late Pleistocene and Holocene paleoenvironments of the north Pacific coast. *Quaternary Science Reviews,* **14,** 449-471 (1995).

McDonald, K.A., P.E.Hennon, J.H. Stevens, and D.W. Green, *Mechanical properties of salvaged dead yellow-cedar in southeast Alaska*, USDA Forest Service, Research Paper FPL-RP-565 (1997).

Mathewes, R.W, A palynoloigcal study of postglacial vegetation in the University Research Forest, southwestern British Columbia, *Can. J. Bot*, **51**, 2085-2103 (1973).

Mathewes, R.W., and L.E. Heusser, A 12, 000 year palynological record of temperature and precipitation trends in southwestern British Columbia, *Canadian Journal of Botany* **59**, 707-710 (1981).

Neiland, B.J, The forest-bog complex in Southeast Alaska, *Vegetatio*, **22**, 1-63 (1971).

Pawuk, W.H, Germination of Alaska-cedar seed, *Tree Planter's Notes*, **44**(1), 21-24 (1993).

Peteet,, D.M., Modern pollen rain and vegetational history of the Malaspina Glacier District, Alaska, *Quaternary Research* **25,** 100-120 (1986).

Puttonen, P., and J.T. Arnott, Influence of photoperiod and temperature on growth, gas exchange, and cold hardiness of yellow cypress stecklings, *Can. J. For. Res*., **24**, 1608-1616 (1994).

Ritland, C., T. Pape, , and K. Ritland, Genetic structure of yellow cedar (*Chamaecyparis nootkatensis*), *Can. J. Bot.*, **79**, 822-828 (2001).

Russell, J.H., Clonal forestry with yellow-cedar Chamaecyparis nootkatensis, Pp. 188-201, In *Clonal forestry, Vol. 2: Conservation and application*, Springer-Verlag, Berlin (1993).

Shaw, C.G. III, A. Eglitis, T.H. Laurent, and P.E. Hennon, Decline and mortality of *Chamaecyparis nootkatensis* in Southeastern Alaska, a problem of long duration but unknown cause. *Plant Dis.*, **69**, 13-17 (1985).

Schaberg, P.G., D.H. DeHayes, and G.J. Hawley, Anthropogenic calcium depletion: a unique threat to forest ecosystem health? *Ecosystem Health,* **7**, 214-228 (2001).

449

_____

Schaberg, P.G., D.H. DeHayes, and G.J. Hawley, P.F. Murakami, G.R. Strimbeck, and S.G. McNulty, Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce, *Can. J. For. Res*., **32**, 1351-1359 (2002).

Schaberg P.G.; P.E. Hennon, D.V. D'Amore, G.J. Hawley, and C.H. Borer, Seasonal differences in freezing tolerance of yellow-cedar and western hemlock trees at a site affected by yellow-cedar decline, *Can. J. For. Res*., **35**, 2065-2070 (2005).

Taylor, T.N., and E.L. Taylor, *The biology and the evolution of plants*, 2nd ed., Cambridge Univ. Press, New York, NY (1993).

Ugolini, F.C., and D.H. Mann, Biopedological origin of peatlands in southeast Alaska, *Nature*, **28**, 366-368 (1979).

Viens, Robert J., *Late Holocene climate change and calving glacier fluctuations along the southwestern margin of the Stikine Icefield, Alaska*, University of Washington, PhD Dissertation, 160 p. (2001).

Warner, B.G., R.W. Mathewes, and J.J Clague, Ice-free conditions on the Queen Charlotte Islands, British Columbia, at the height of late Wisconsin glaciation. *Science* **218,** 675-677. (1982).

Wittwer, D. (comp.), *Forest health conditions in Alaska*, 2004, USDA For. Serv., Alaska Region, Protection Report R10-PR-3, Anchorage, AK, 96p., (2004).

_____

450