United States
Department of
Agriculture

Forest Service

Pacific
Northwest
Region

February 2006

Whitebark Pine in Washington and Oregon

A synthesis of current studies and historical data

Pacific Northwest Albicaulis Project

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Whitebark pine *(Pinus albicaulis)* at sunset, Tyee Mountain, Okanogan and Wenatchee National Forests

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Abstract

Whitebark pine (*Pinus albicaulis* Englem.) is an important component of high-elevation communities in the northwestern United States and southwestern Canada. The species has suffered substantial declines in recent decades through the combined effects of fire suppression, mountain pine beetle (*Dendroctonus ponderosae*), and the introduced pathogen, white pine blister rust (*Cronartium ribicola*). Recent concern over the status of whitebark pine has motivated land managers to initiate the development of plans to sustain and restore the species in Washington and Oregon. Most research documenting the status and restoration requirements of whitebark pine has occurred in the Intermountain West. Greater understanding of the status and biological needs of this species in the Pacific Northwest will assist land managers in developing a management plan that is appropriate for the region. This document discusses current and historical information on the distribution of whitebark pine populations, the introduction and spread of blister rust, stand health inventories, regeneration potential and population trends, genetic variation, and fire history regimes from studies specific to Washington and Oregon. Results of recorded observations of whitebark pine mortality and the prevalence of blister rust infection in Washington and Oregon from 1937 to the present are summarized.

The Pacific Northwest Albicaulis Project of the USDA Forest Service endeavors to support the conservation and restoration of whitebark pine ecosystems in Oregon and Washington through field and laboratory studies, publications, and development of management strategies.
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February 2006

Acknowledgements

The authors are grateful to all those who helped to improve this work. Tom DeSpain, Dave Doede, Vicky Erickson, Jim Hadfield, Blakey Lockman, Michael Murray, Mike Roantree, Regina Rochefort, and Bryce Richardson generously shared their knowledge and data, and reviewed earlier drafts of this document. Any remaining errors or inconsistencies are the responsibility of the authors.

Edited by Mary Carr, CAT Publishing Arts.

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Introduction

Whitebark pine (*Pinus albicaulis*) is an essential component of forested communities of the subalpine mountains of western North America. Its unusually large seeds, unique seed dispersal system, and extreme stress tolerance have several ecological consequences that make this tree essential to the health of subalpine ecosystems (Tomback et al. 2001).

The large, wingless seeds of whitebark pine are a highly prized food for grizzly bears (*Ursus arctos horribilis*) (Mattson et al. 2001) as well as for black bears (*U. americanus*), pine squirrels (*Tamiasciuris* spp.), golden-mantled ground squirrels (*Spermophilus lateralis*), Clark's nutcrackers (*Nucifraga columbiana*), and many other small birds and mammals (Tomback and Kendall 2001).

While most conifers are wind-dispersed, whitebark pine relies on a mutualistic relationship with a single species of bird, the Clark's nutcracker, for seed dispersal (Hutchins and Lanner 1982). The nutcracker harvests seeds from the indehiscent cones and caches the seeds, some of which later germinate. The bird's long flight distances and tendency to cache seeds in open areas (Tomback 1986, 2001) mean whitebark pine is often the first conifer to establish after disturbance, thus playing an important role in plant community recovery (Tomback et al. 2001).

Although whitebark pine is an early successional species at lower elevations, its stress tolerance (McCune 1988) allows it to form climax stands in the harsh, windy conditions at treeline (Arno 2001). Because few other trees can persist in these conditions, whitebark pine's role in reducing soil erosion and runoff is crucial in protecting high-elevation watersheds (Tomback et al. 2001).

As a result of the restriction of whitebark pine to high-elevation sites, the range of the species in the Cascade mountains of the Pacific Northwest is separated from its range in the Rockies by the extensive lowlands of the Columbia Plateau (fig. 1). A few isolated stands loosely connect the western and eastern portions of the range in southeastern British Columbia and northeastern Washington (McCaughey and Schmidt 2001). Disjunct populations occur in the Blue Mountains of eastern Oregon and in the northeastern portion of the Olympic Mountains in Washington State.

In Washington and Oregon, the dry, high-elevation habitats that favor this tree species occur in pockets or swathes on ridges and peaks. Whitebark pine populations therefore tend to be scattered and patchy in the region (Morgan and Murray 2001). These patches occur frequently east of the crest of the Cascade Range but occurrence decreases with increasing rainfall near and west of the crest.

Whitebark pine occurs on a wide variety of site and stand conditions in the Pacific Northwest. In droughty regions such as the eastern Cascades, whitebark pine can occur as a climax species. On particularly harsh and rocky sites, whitebark pine may be the only tree species capable of thriving while in other conditions it co-occurs in mixed stands with lodgepole pine and other conifers. On wetter, more productive sites such as those in the western Cascades, whitebark pine communities may be early to mid successional, eventually displaced by more shade-tolerant species (Arno 2001). While historical fire regimes vary widely across the region, the persistence of whitebark pine in seral habitats may depend on openings created by periodic fires or other disturbances.

The past 50 years have witnessed a dramatic decline in whitebark pine stands (Arno 1986, Keane and Arno 1993, Kendall and Arno 1990) due to the combined effects of fire suppression, mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, and infection by white pine blister rust, a disease caused by the introduced fungal pathogen *Cronartium ribicola* (Keane et al. 1990, Keane and Morgan 1994).

Recent concern over the status of this important tree has prompted a call for active management from both academic and agency scientists (Tomback et al. 2001). Management plans designed to sustain and restore the species in Oregon and Washington would benefit from a greater understanding of the status and biological needs of the species in the region.

Most research quantifying the health of whitebark pine stands and exploring the effectiveness of silvicultural and genetic restoration techniques has occurred in the Intermountain West—Idaho, Montana, and Wyoming. Although much of this research is likely to be relevant throughout the range of whitebark pine, the unique aspects of whitebark pine ecology in the Pacific Northwest warrant a review of studies that have been done in Oregon and Washington. The greater population isolation (Morgan and Murray 2001) and increased prevalence of early successional communities in the region combined with the favorable influence of humidity on blister rust transport and infection (Arno and Hoff 1990, McDonald and Hoff 2001, Kinloch 2003) may translate to differences in population dynamics and genetics (Morgan and Murray 2001), community ecology and optimal fire regime (Siderius and Murray 2004), and vulnerability to blister rust (Hoff and Hagle 1990, Kendall and Keane 2001).

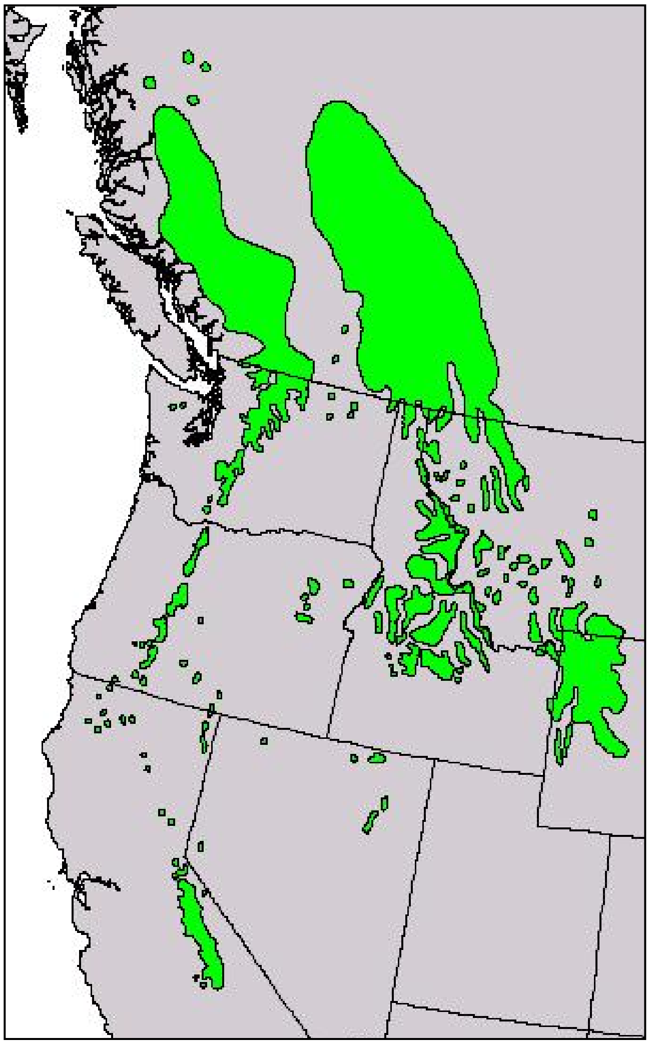


Figure 1. Range of whitebark pine (U.S. Geological Survey, 1999, Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr. (Little 1971))

This paper synthesizes recent work and historical information on the distribution of whitebark pine populations, the introduction and spread of blister rust, the health of whitebark pine stands, regeneration potential and population trends, patterns of genetic variation and preliminary studies documenting the fire regime in these two states.

Synthesis of current information in the Pacific Northwest

Whitebark pine distribution in Washington and Oregon

Analysis of the USDA Forest Service’s Current Vegetation Survey (CVS) data indicates that the species’ lower elevational limit varies across the region from around 4,800 feet in the Cascades to around 5,700 feet in the Blue Mountains in northeast Oregon. Its narrow elevational tolerance restricts the species’ distribution to remote mountainous areas, almost entirely on public lands (fig. 2). In Washington and Oregon, whitebark pine occurs in montane habitats on all national parks, some Indian reservation lands, and all national forests except the Siuslaw and Ochoco National Forests (Sniezko et al. 1994).

The range map created by Little (1971) provides a generalized outline of whitebark pine distribution (fig. 1, above). In an effort to display more precisely the known and potential distribution of whitebark pine in national forests of Washington and Oregon, we are developing a new distribution map based on documented presence and absence of whitebark pine, and on topographic and climate parameters, including elevation and precipitation (fig. 2).

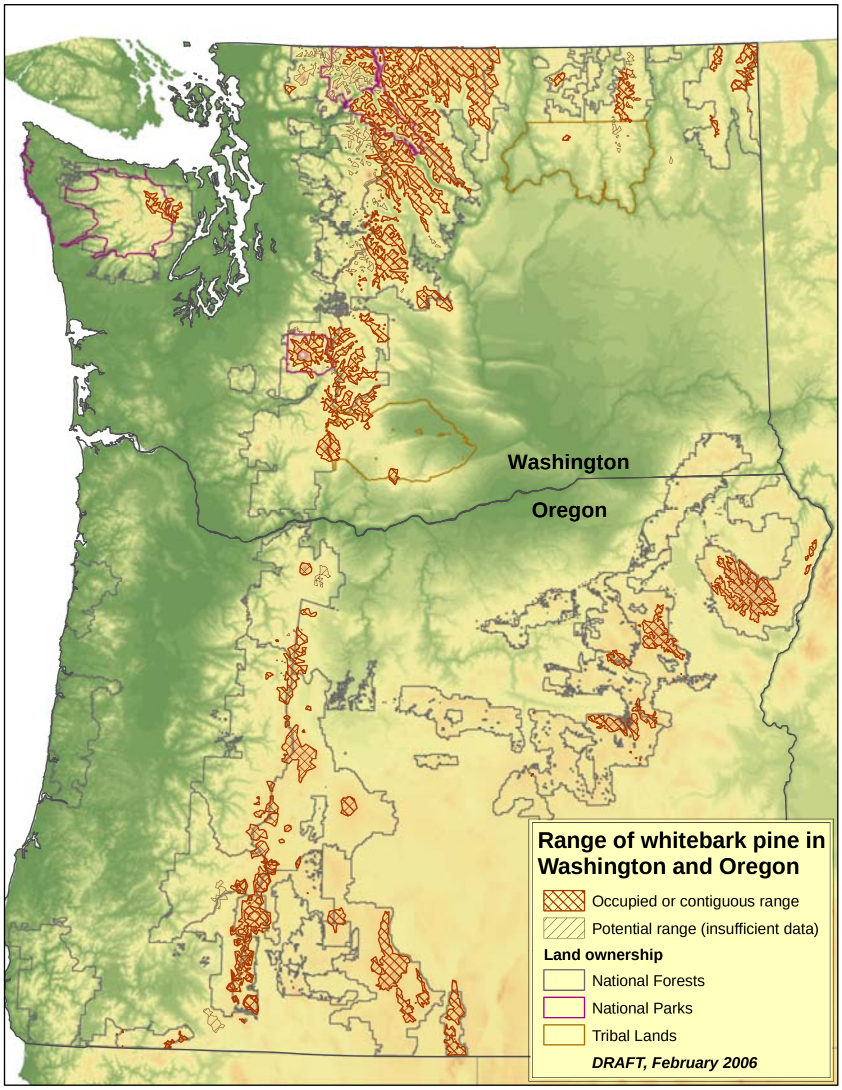
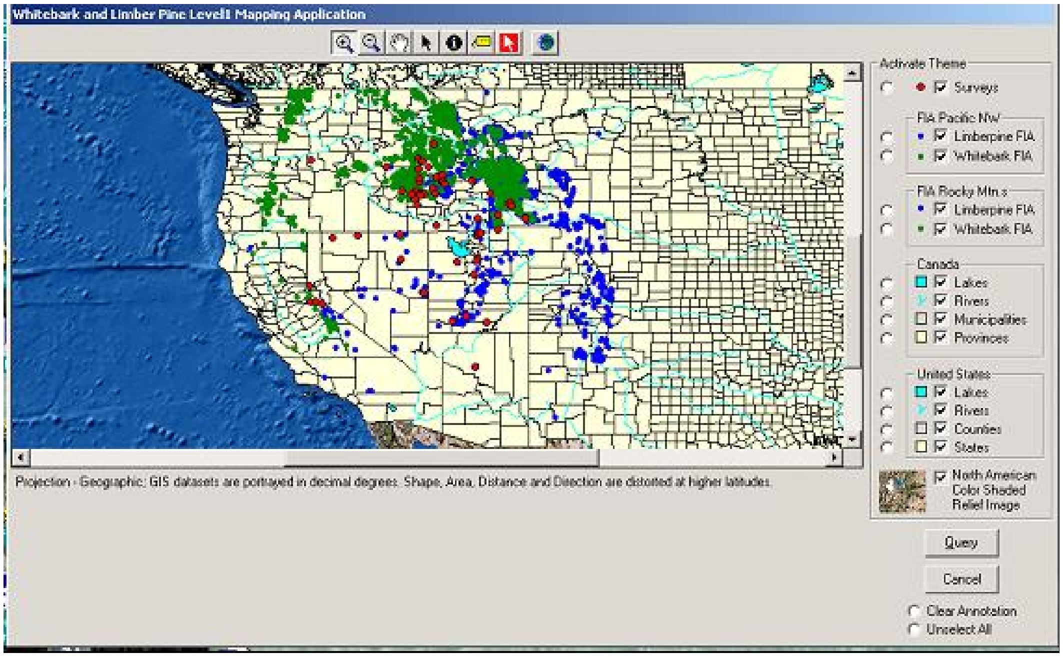


Figure 2. Range of whitebark pine in Washington and Oregon (Shoal, in preparation)

Data used to develop this map include CVS plot data for all national forests in the two states, Forest Service ecology plot and other data, and sites outside of national forest boundaries where whitebark pine occurrence has been documented. On this map the range of whitebark pine is divided into two categories: (1) areas of occupied or contiguous habitat; and (2) areas of potential habitat—where conditions appear favorable for whitebark pine, but presence or absence has either not yet been documented (on national forests) or where data were insufficient or unavailable. At the time of this writing, the map is in draft form and is undergoing review and revision.

In the national parks, North Cascades National Park and Mt. Rainier National Park have developed detailed vegetation maps showing 9,691acres (3,922 ha) and 2,809 acres (1,137 ha) of whitebark pine stands, respectively (Agee et al. 1985, Rochefort 1995b). In Mt. Rainier National Park, these stands—ranging in size from 5 acres (2 ha) to hundreds of acres each—have been digitized and entered into a Geographic Information System (GIS) (Rochefort 1995b). Using aerial photographs verified by ground counts, Cottone and Ettl (2001) estimated that 21,029 whitebark pine individuals occur in Mt. Rainier National Park. Mapping of whitebark pine stands in Crater Lake National Park is on schedule to be completed in 2007 (Murray, personal communication, 2005).

Forest Service Forest Inventory and Analysis (FIA) plot data currently are being used to develop a range-wide GIS database (Lockman et al. 2004) on the distribution and condition of whitebark pine (fig. 3). This database is near completion and is in the beta-testing phase (Lockman, personal communication 2005).



Projection - Geographic; GIS datasets are portrayed in decimal degrees. Shape, Area, Distance and Direction are distorted at higher latitudes.

Figure 3. Geographic Information System (GIS) data on the distribution of whitebark pine. Extracted from the Whitebark and Limber Pine Level 1 database currently under development (Lockman et al. 2004). Whitebark pine locations are indicated in green, limber pine in blue.

White pine blister rust in the Pacific Northwest

White pine blister rust is a fungal pathogen that infects most five-needle pines (*Pinus*subgenus *Strobus*) and plants in the gooseberry/currant genus (*Ribes* spp.) and has been recently found to infect and sporulate on sickletop lousewort (*Pedicularis racemosa)* and scarlet Indian paintbrush (*Castilleja miniata)* (McDonald et al. 2006). The disease was introduced to western North America from Eurasia in 1910 (McDonald and Hoff 2001); however, it was not discovered until 1921 when it was found on cultivated black currants (*Ribes nigrum*) in Vancouver, British Columbia (Eastham 1922). Blister rust was first recorded in native whitebark pine stands 100 miles north of Vancouver in the Coast Range of British Columbia in 1926 (Lachmund 1926). By 1943 researchers had documented the spread of the disease southward as far as Mt. Jefferson in Oregon (Bedwell and Childs 1943).

Although the first reports of the disease began in the 1920s, backdating infection points revealed that natural stands had been affected by white pine blister rust several years earlier (Lachmund 1933). The earliest infection in Washington occurred in 1913 on western white pine (*Pinus monticola*) in the North Cascades near Newhalem. By 1918 the pathogen had spread as far south as Minto Creek, 50 miles east of Salem in the Oregon Cascades (Hadfield 2000). By 1927, blister rust had become established in most of the range of whitebark pine (Hoff and Hagle 1990). Hadfield (2000) hypothesized that most whitebark pine stands in Washington and northern Oregon had been exposed to many pulses of infection from 1921 to 1936.

Recent dendrochronological studies from whitebark pine stands Washington provide further evidence for the timing and geographic pattern of past blister rust infections. DelPrato (1999) reported rust-induced growth-reduction waves beginning in 1933 in the northwest corner of Mt. Rainier National Park and spreading to the south from there. The pattern of waves in growth reduction across the study area suggested a history of multiple localized infections, possibly related to local climate effects. In a 160-mile north-south transect on the Okanogan, Mt. Baker-Snoqualmie, and Wenatchee national forests, 27 percent of the 89 trees sampled exhibited growth suppressions (King 2004, 2005). These growth suppressions were mostly confined to the most recent 80 years of the 200-year record represented in the samples. They first appear in the record in the 1920s, coincident with the purported first appearance of blister rust in the state.

Although blister rust has long been established throughout the range of whitebark pine (Hoff and Hagle 1990), the epidemic is still spreading into environments previously considered inhospitable (Kinloch 2003), with devastating effects on the health of this tree species in the Pacific Northwest as in other regions. By 1993, land managers across Washington and Oregon had observed widespread damage from blister rust and bark beetles in the central and northern Cascades, the Olympics, and in northeastern Washington and eastern Oregon (Sniezko et al. 1994).

Stand health inventories in the Pacific Northwest

Only two health assessments of whitebark pine were conducted in the Pacific Northwest prior to 1992. From 1937 to 1939, Bedwell and Childs (1943) recorded the percentage of trees infected and the number of cankers observed for trees on the Olympic, Wenatchee and Mt. Hood national forests and the Warm Springs Indian Reservation (table 1). Gynn and Chapman (1951 and 1952, cited in Hoff and Hagle 1990) measured the number of trees infected with blister rust in Mt. Rainier National Park. From 1994 to the present, whitebark pine stand health assessments reporting mortality rate and the prevalence of blister rust infection have been conducted across the range of whitebark pine in Oregon and Washington (tables 1 and 2). Where possible, and with permission of the authors, results from these studies have been standardized here for ease of comparison as described below. See Appendix A for detailed summaries of the methods used within each study and the original results reported.

The various authors used different analytical approaches to calculate mortality and infection rates. For example, some reported the percentage of living trees infected (Bedwell and Childs 1943; Doede, unpublished data; Erickson, unpublished data), while others reported the percentage of living infected trees among all living and dead trees encountered (Murray and Rasmussen 2003; Shoal and Aubry 2004; Acker and Shoal, unpublished data; Rochefort, unpublished data; Shoal and Aubry, unpublished data). The latter approach results in underestimation of the infection rate. The raw data were reanalyzed here to report the prevalence of blister rust infection for all studies as the percentage of living trees infected (infected living trees/all living trees) (table 1). In some cases the raw data were not available for recalculation (Gynn and Chapman 1951 and 1952, cited in Hoff and Hagle 1990; Hoff 1992, cited in Kendall 1994a andb; Hadfield et al. 1996; Goheen et al. 2002).

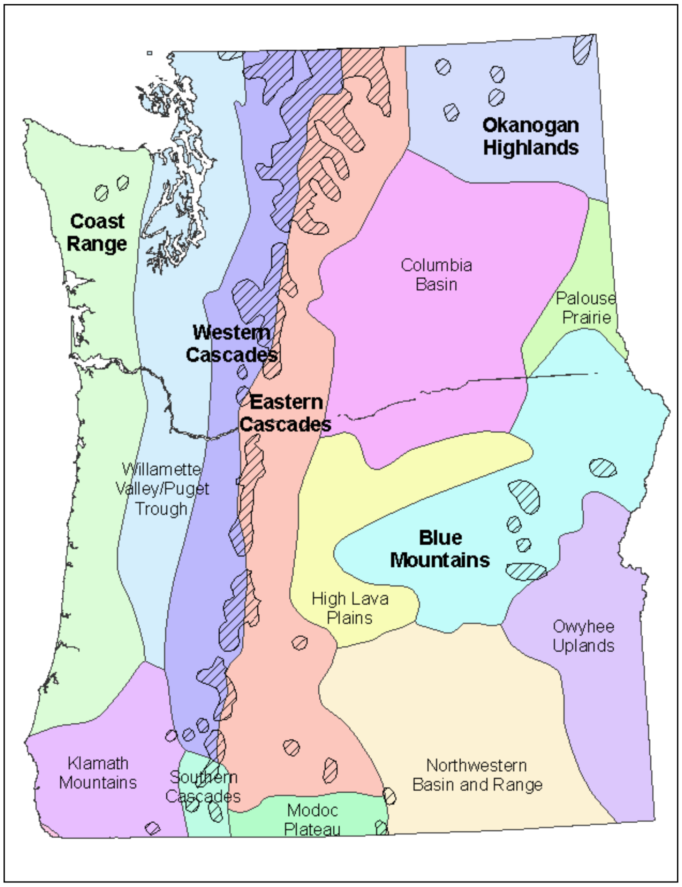


Figure 4. Bailey's ecoregions and the distribution of whitebark pine in Washington and Oregon. Whitebark pine distribution is from Little (1971). Ecoregions with data in tables 1 and 2, and figures 5 and 6 (below) are shown with bold labels.

Data from multiple samples were summarized differently in the original sources as well. For example, some authors reported the percentage of affected trees when all transects were pooled across a forest (Goheen et al. 2002; Erickson, unpublished data) while others reported the percentage of affected trees per acre (Doede, unpublished data) or per survey unit (Shoal and Aubry 2004). The raw data were reanalyzed here so that results from all studies could be reported in the same unit: the average percent of affected trees per stand. Summarizing the data on a per-stand basis has the advantage of capturing the amount of variation observed within individual studies by calculating the standard deviation. Mean, standard error, and standard deviation were calculated here following the ratio of means method (Cochran 1977, equations 3.31 and 3.34). This method is generally recommended in the survey sampling literature (Max, personal communication, 2005) for estimation of a ratio based on a cluster sample where clusters differ in size (that is, for estimation of a percentage based on sampled stands where the number of trees sampled per stand varies). The data required for this recalculation were available for all studies sampling more than one stand except the study conducted on the Umpqua National Forest (Goheen et al. 2002).

Data in tables 1 and2 and figures 5 and 6 are grouped by Bailey’s ecoregion sections (fig.4, above). An ecoregion is a relatively large unit of land or water containing geographically distinct assemblages of species, natural communities, and environmental conditions (World Wildlife Fund 2005). Bailey’s classification is a hierarchical system with four levels. From largest to smallest, the levels are domains, divisions, provinces and sections (USDA Forest Service Inventory and Monitoring Institute 2004).

The prevalence of blister rust infection

Blister rust infection is widespread in whitebark pine stands from northern Washington to south-central Oregon (table 1 and fig. 5). The pathogen was detected in all but 6 of the more than 170 stands surveyed. Blister rust was not observed in 1 stand in North Cascades National Park, 2 stands in Mt. Rainier National Park, 1 stand on the Wenatchee National Forest, 1 stand in Crater Lake National Park, and 1 stand on the Malheur National Forest. The average percentage of infected living trees per stand (for stands that had infected treees) ranged from 11 to 95 percent.

No obvious latitudinal or longitudinal patterns in mortality or blister rust incidence are evident from studies done to date. This is in contrast to predictions that the prevalence of blister rust in whitebark pine in the Cascade Range would decline from north to south (Kendall and Keane 2001, Campbell and Antos 2000). Instead, the high degree of variation in average infection rates within ecoregions and among individual stands within studies suggests that there is a high degree of localized variation in the prevalence of blister rust infection across the region. Often the percentage of infected trees varied widely even among transects within close proximity (Shoal and Aubry 2004). This corroborates observations that the geographic scale of infection is very localized (DelPrato 1999) and that “hot spots” of higher damage can occur in the Cascades (Kendall and Keane 2001) even in areas of moderate infection.

It has been predicted that high humidity and heavy rainfall of the Olympic Mountains would cause a disproportionately high infection rate (Kendall and Keane 2001, Tomback et al. 2001) because humidity favors blister rust spore transport from one host to another (Arno and Hoff 1990, McDonald and Hoff 2001, Kinloch 2003) and the probability of waves of infection increases as the climate becomes cooler and more moist (Kinloch 2003). However, the prevalence of blister rust infection on the Olympic Peninsula was similar to that of other areas in the Pacific Northwest.

Mortality

The highest recorded overall mortality for an individual stand was 92 percent (table 2, fig. 6) and the lowest was 0 percent (table 2). The average mortality per stand ranged from 2 to 41 percent. These figures include mortality from all causes. No latitudinal or ecoregional pattern was evident.

Because most surveyors did not report how recently dead trees had been killed, the number of dead trees at a site may not reflect recent mortality rates, and is not a reliable indicator of mortality due to blister rust. Decomposition of dead trees can take many decades, particularly in high-elevation whitebark pine sites in the Cascades (Hadfield

2000). Furthermore, dead trees may have succumbed to something other than blister rust. Mountain pine beetle epidemics have periodically decimated whitebark pine stands, so standing dead trees could be relicts of beetle outbreaks that occurred many decades ago, perhaps prior to the local advent of blister rust. Distinguishing between old dead and recently killed trees (Hadfield et al. 1996, Hadfield 2000) could shed light on mortality rates in response to current levels of attack by rust and beetles. Hadfield (2000) estimated that about 12 percent of the whitebark pine mortality in 16 sites he surveyed in Washington had occurred in the previous 5 years.

Other damaging agents

Mountain pine beetle (*Dendroctonus ponderosae*) and dwarf mistletoe (*Arceuthobium* spp.) are two additional threats to whitebark pine; both can cause heavy mortality to whitebark pine stands or increase their susceptibility to other diseases (Kendall and Keane 2001). Before the introduction of blister rust, mountain pine beetle was the most significant natural damaging agent to whitebark pine (Perkins and Roberts 2003). Widespread mountain pine beetle epidemics have periodically swept upward from low-elevation lodgepole pine stands into higher whitebark stands, with peaks in the 1930s and 1940s and in the 1970s and 1980s (Arno and Hoff 1990).

Stand health assessments recording mountain pine beetle and mistletoe presence in Washington and Oregon have not documented recent major impacts from either species. Between 1998 and 2004, mountain pine beetle was recorded on the Okanogan, Wenatchee, Olympic, Mt. Hood, and Umpqua national forests and in Crater Lake National Park (Goheen et al. 2002; Murray and Rasmussen 2003; Shoal and Aubry 2004; Doede, unpublished data). Within each location, the extent of beetle attack varied from very localized (only a single stand in Crater Lake National Park (Murray and Rasmussen 2003)) to widespread (75 percent of stands on the Okanogan National Forest (Shoal and Aubry 2004)). The intensity of attack varied as well, with the prevalence of beetle-attacked whitebark pine ranging from 0.4 percent of surveyed clumps on the Olympic National Forest (Shoal and Aubry 2004) to 15.0 percent of trees in the one stand in Crater Lake National Park. Very little mortality was attributed to mountain pine beetle in stand health assessments, although most authors mentioned that cause of death was often difficult to determine. Thirteen percent of the total whitebark pine mortality on the Umpqua National Forest was caused by mountain pine beetle alone, and 18 percent resulted from a combination of beetle attack and rust infection; however, total mortality was only 10 percent of the trees sampled in the study (Goheen et al. 2002). Informal field observations in 2005 indicate that mountain pine beetle occurrence in whitebark pine is increasing on the Okanogan and Wenatchee national forests. There has also been a noticeable increase in beetle-caused mortality between 2003 and 2005 at Crater Lake National Park (Murray, personal communication, 2005).

Table 1. Prevalence of blister rust infection documented in stand assessments conducted in Washington and Oregon from 1937 to 2004

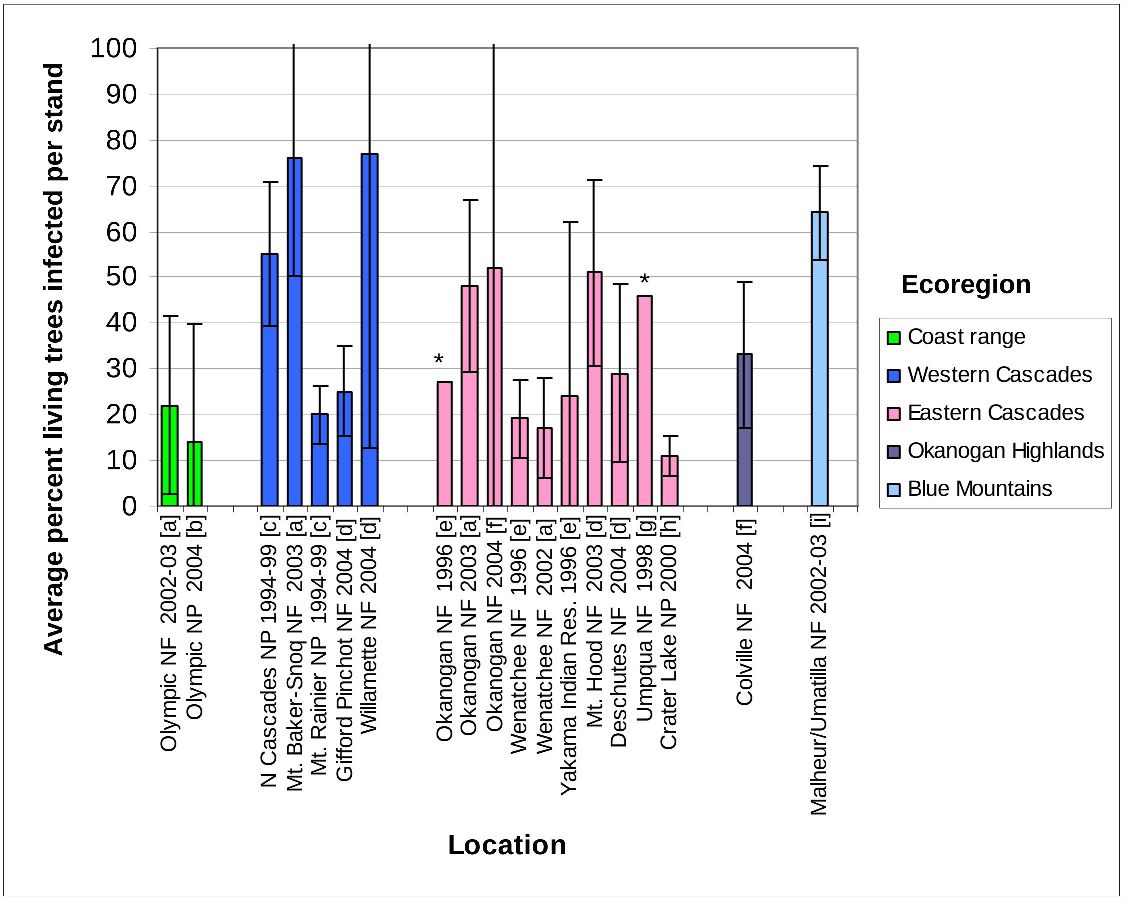
Ecoregion section (Bailey's)	Forest/Park	Year of survey	Location	No. transects or plots	Total living stems (or clumps) sampled	Percent living stems infected per stand		s.e.[a]	std[a]	Source
						Range	Mean[a]			
Coast Range	Olympic NF	1937-39	Marmot Pass, WA	1	26	**--**	**92**	--	--	Bedwell & Childs 1943
	Olympic NF	2002-03	5 stands	5	241 clumps	**11 – 49**	**22**	7	15	Shoal & Aubry 2004[b]
	Olympic NP	2004	3 stands	3	259 clumps	**4 – 32**	**14**	6	11	Acker & Shoal, unpublished data[b]
Western Cascades	N Cascades NP	1994-99	10 stands	13	378	**0 – 74**	**55**	7	24	Rochefort, unpublished data[b]
	Mt. Baker-Snoq NF	2003	3 stands	3	127 clumps	**65 – 84**	**76**	6	11	Shoal & Aubry 2004[b]
	Mt. Rainier NP	1951-52	Mt. Rainier, WA	--	899[c]	**52 – 55[c]**	**54[c]**	1	2	Gynn & Chapman 1951&52 in Hoff and Hagle 1990
	Mt. Rainier NP	1992	Sunrise Ridge, WA	--	--	**--**	**95[d]**	--	--	Hoff 1992 in Kendall 1994a & b
	Mt. Rainier NP	1994-99	18 stands	61	977	**0 – 55**	**23**	4	16	Rochefort, unpublished data[b]
	Gifford-Pinchot NF	2004	7 stands	7	196 clumps	**8 – 57**	**25**	4	10	Doede, unpublished data
	Mt. Hood NF	1937-39	Salmon River, OR	1	17	**--**	**94**	--	--	Bedwell & Childs 1943
	Willamette NF	2004	3 stands	3	102 clumps	**47 – 100**	**77**	15	26	Doede, unpublished data
Eastern Cascades	Okanogan NF	1996	Trinity Mt, WA	1	102	**--**	**27[d]**	--	--	Hadfield et al. 1996
	Okanogan NF	2003	8 stands	8	369 clumps	**21 – 84**	**48**	8	23	Shoal & Aubry 2004[b]
	Okanogan NF	2004	2 stands	2	62	**31 – 73**	**52**	21	30	Shoal & Aubry, unpublished data[b]
	Wenatchee NF	1937-39	Hyas Lake, WA	1	9	**--**	**89**	--	--	Bedwell & Childs 1943
	Wenatchee NF	1996	3 stands	3	227	**16 – 21[e]**	**19[d]**	2	4	Hadfield et al. 1996
	Wenatchee NF	2002	12 stands	19	885	**0 – 67**	**17**	5	17	Shoal & Aubry 2004[b]
	Yakama Indian Res.	1996	2 stands	2	94	**21 – 28[e]**	**24[d]**	3	5	Hadfield et al. 1996
	Mt. Hood NF	1937-39	2 stands	2	36	**88 – 100**	**92**	5	7	Bedwell & Childs 1943
	Mt. Hood NF	2003	10 stands	10	358 clumps	**23 – 90**	**51**	9	29	Doede, unpublished data
	Warm Springs Res.	1937-39	Mt. Wilson, OR	1	17	**--**	**71**	--	--	Bedwell & Childs 1943
	Deschutes NF	2004	5 stands	9	299 clumps	**16 – 60**	**29**	7	16	Doede, unpublished data
	Umpqua NF	1998	21 stands	21	--	--	**46[e]**	--	--	Goheen et. al 2002
	Crater Lake NP	1992	Crater Lake, OR	--	--	**--**	**47[d]**	--	--	Hoff 1992 in Kendall 1994a&b
	Crater Lake NP	2000	15 stands	22	965	**0 – 27**	**11**	2	8	Murray and Rasmussen 2003[b]
Okanogan Highlands	Colville NF	1992	Salmo Mtn, WA	1	--	**--**	**75[d, f]**	--	--	Hoff 1992 in Kendall 1994b
	Colville NF	2004	4 stands	4	171	**23 – 44**	**33**	5%	10%	Shoal & Aubry, unpublished data[b]
Blue Mountains	Umatilla/Malheur NF	2002-03	30 stands	153	870	**0 – 100**	**64**	5%	29%	Erickson, unpublished data[b]

Notes for table 1.

[a] Values are recalculated from published data and with the permission of authors of unpublished data to report the average and variation in blister rust prevalence on a per stand basis. Mean, standard error (s.e.) and standard deviation (std) are calculated following the ratio of means method (Cochran 1977, p. 66, equations 3.31 and 3.34).
[b] Percentages in the original source were calculated as the percent of living stems infected among all living and dead stems encountered (#living stems infected/all living + dead stems encountered). With permission of the authors, percentages are recalculated here as the percentage of living stems only that are infected (#living stems infected/living stems encountered).
[c] Original source not examined. Percentage and sample size may include dead stems.
[d] Percentages in the original source may have included dead stems. Raw data was not available for recalculation.
[e] Percentage is not the average as calculated by the ratio of means, it is the percentage reported in Goheen et al. (2002), which is the percentage of all living infected trees among all living and dead trees encountered when all 21 transects are pooled.
[f] Data are reported for seedlings only.

Survey results presented in table 1 are grouped by Bailey's ecoregion (Bailey 1995) and by national forest, national park, or Indian reservation. Within an ecoregion, surveys are listed in order generally from north to south. Surveys conducted in forests or parks spanning more than one ecoregion were assigned to an ecoregion based on maps or habitat descriptions included in the original sources cited.

Methods and results reported in the original sources are summarized in Appendix A. With the authors' permission, values from original sources were recalculated using the ratio of means method (Cochran 1977) to report the average percent of living trees that are infected within stands at each location.



Source	**Notes**
[a] Shoal and Aubry (2004)[1]	*Percentages are based on counts of clumps of aggregated stems (avg stems/clump = 3.4. 25 percent of clumps were comprised of a single stem).*
[b] Acker and Shoal (unpub. data)[1]	*Percentages are based on counts of clumps of aggregated stems (avg stems/clump = 3.6. 35 percent of clumps were comprised of a single stem).*
[c] Rochefort (unpublished data)[1]	
[d] Doede (unpublished data)	
[e] Hadfield et al. (1996)	*Percentages in the original source may have included dead stems in the numerator and denominator. Raw data were not available for reanalysis. (Hadfield, personal communication 2005)*
[f] Shoal & Aubry (unpub. data)[1]	
[g] Goheen et al. (2002)	*Percentage is not the average as calculated by the ratio of means; it is the percentage reported in the original source, which is the percentage of all living infected trees among all living and dead trees encountered when all 21 transects were pooled.*
[h] Murray & Rasmussen (2003)[1]	
[i] Erickson, (unpublished data)[1]	

[1] Percentages in the original source were calculated as the percent of living stems infected among all living and dead stemsencountered (#living stems infected/all living + dead stems encountered). With permission of the authors, percentages are recalculated here as the percentage of living stems only that are infected (#living stems infected/living stems encountered).

Figure 5. Prevalence of blister rust infection documented in stand assessments conducted in Washington and Oregon from 1994 to 2004. Within each ecoregion, survey results are listed in order from north to south. With the authors' permission, values from original sources were recalculated using the ratio of means method (Cochran 1977) to report the average percent of living trees infected within stands at each location. Ninety-five percent confidence intervals are shown by the vertical bars. Studies for which confidence intervals were not calculated are indicated by an asterisk.

Table 2. Mortality documented in stand assessments conducted in Washington and Oregon from 1992 to 2004

Ecoregion section (Bailey's)	Forest/Park	Year of survey	Location	No. transects or plots	Sample size (stems)	Percent mortality per stand		s.e.[a]	std[a]	Source
						Range	Mean[a]			
Coast Range	Olympic NF	2002-03	3 stands	3	598	**8 – 46**	**25**	12	21	Shoal & Aubry 2004
	Olympic NP	2004	3 stands	3	952	**2 – 28**	**21**	7	13	Acker & Shoal unpublished data
Western Cascades	N Cascades NP	1994-99	10 stands	13	506	**3 – 92**	**26**	12	39	Rochefort, unpublished data
	Mt. Baker-Snoq NF	2003	3 stands	3	752	**26 – 53**	**41**	8	13	Shoal & Aubry 2004
	Mt. Rainier NP	1992	Sunrise Ridge, WA	--	--	**--**	**25**[b]	--	--	Hoff 1992 in Kendall 1994a & b
	Mt. Rainier NP	1994-99	18 stands	61	1641	**13 – 84**	**41**	4	17	Rochefort, unpublished data
	Gifford Pinchot NF	2004	7 stands	7	479	**0 – 55**	**40**	5	12	Doede, unpublished data[c]
	Willamette NF	2004	3 stands	3	346	**31 – 49**	**38**	5	9	Doede, unpublished data[c]
Eastern Cascades	Okanogan NF	1996	Trinity Mt., WA	1	104	**--**	**2**	--	--	Hadfield et al. 1996
	Okanogan NF	2003	8 stands	8	1122	**6 – 42**	**16**	4	11	Shoal & Aubry 2004
	Okanogan NF	2004	2 stands	2	92	**14 – 45**	**33**	15	22	Shoal & Aubry, unpublished data
	Wenatchee NF	1996	3 stands	3	257	**8 – 14**	**12**	2	4	Hadfield et al. 1996
	Wenatchee NF	2002	1 stand	1	110	**--**	**40**	--	--	Shoal & Aubry 2004
	Yakama Ind. Res.	1996	2 stands	2	101	**6 – 8**	**7**	1	1	Hadfield et al. 1996
	Mt. Hood NF	2003	10 stands	10	1583	**5 – 89**	**40**	12	39	Doede, unpublished data[c]
	Deschutes NF	2004	5 stands	9	852	**19 – 51**	**33**	6	14	Doede, unpublished data[c]
	Umpqua NF	1998	21 stands	21	--	--	**10**[c]	--	--	Goheen et. al 2002
	Crater Lake NP	1992	Crater Lake, OR	--	--	--	**5**[b]	--	--	Hoff 1992 in Kendall 1994a&b
	Crater Lake NP	2000	15 stands	22	1100	**4 – 29**	**12**	3	10	Murray and Rasmussen 2003
Okanogan Highlands	Colville NF	2004	4 stands	4	225	**20 – 33**	**24**	4	7	Shoal & Aubry, unpublished data
Blue Mountains	Umatilla/Malheur NF	2002-03	30 stands	153	1146	**0 - 68**	**24**	3	17	Erickson, unpublished data

[a] *Values are recalculated from published data and with the permission of authors of unpublished data to report the average and variation in mortality on a per stand basis. Mean, standard error (s.e.) and standard deviation (std) are calculated following the ratio of means method (Cochran 1977, p. 66, equations 3.31 and 3.34).*

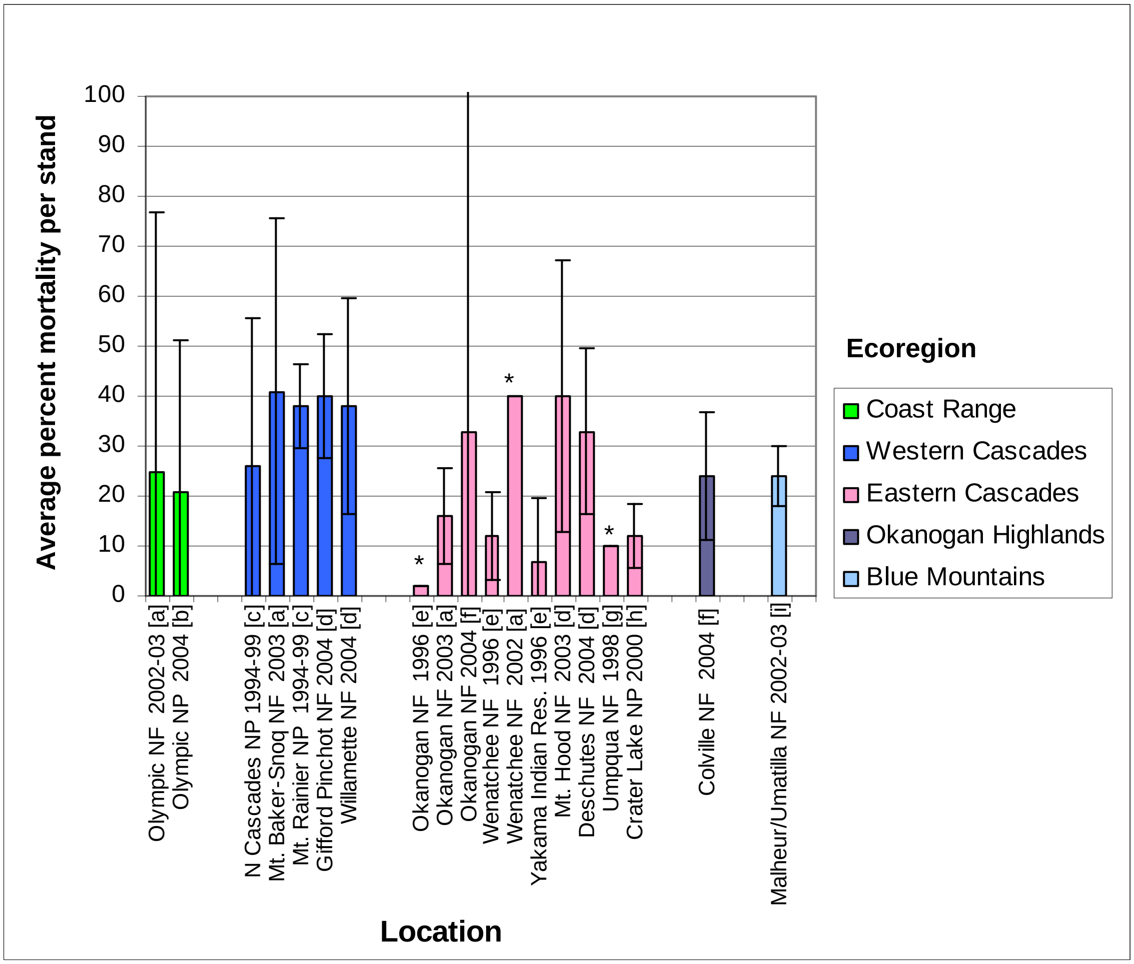
[b] *Percentage is not the average as calculated by the ratio of means, it is the percentage reported in Kendall 1994a, 1994b, with no methods given.*

[c] *Percentages in the original source were reported as the percentage of dead stems per acre. With permission of the author, percentages are recalculated here without acreage.*

[d] *Percentage is not the average as calculated by the ratio of means, it is the percentage reported in Goheen et al. 2002, which is the percentage of all dead trees among all live and dead trees encountered when all 21 transects are pooled.*

Survey results are grouped by Bailey's ecoregion (Bailey 1995) and by national forest, national park, or Indian reservation. Within an ecoregion, surveys are listed in order generally from north to south. Surveys conducted in forests or parks spanning more than one ecoregion were assigned to an ecoregion based on maps or habitat descriptions included in the original sources cited.

Methods and results reported in the original sources are summarized in Appendix A. With the authors' permission, values from original sources were recalculated using the ratio of means method (Cochran 1977) to report the average percent mortality within stands at each location.



Source	***Notes***
[a] Shoal and Aubry (2004)	
[b] Acker and Shoal (unpub. data)	
[c] Rochefort (unpublished data)	
[d] Doede (unpublished data)	*Percentages in the original source were reported as the percentage of dead stems per acre. With permission of the author, percentages are recalculated here without acreage.*
[e] Hadfield et al. (1996)	
[f] Shoal & Aubry (unpub. data)	
[g] Goheen et al. (2002)	*Percentage is not the average as calculated by the ratio of means; it is the percentage reported in the original source, which is the percentage of all dead trees among all living and dead trees encountered when all 21 transects were pooled.*
[h] Murray & Rasmussen (2003)	
[i] Erickson, (unpublished data)	

Figure 6. Mortality documented in stand assessments conducted in Washington and Oregon from 1994 to 2004. Within each ecoregion, survey results are listed in order from north to south. Values from original sources were recalculated from original sources with the authors' permission to report the average percent mortality within stands (Cochran 1977) at each location. Ninety-five percent confidence intervals are shown by the vertical bars. Studies for which confidence intervals were not calculated are indicated by an asterisk.

Population trends and regeneration potential

Cottone (2001) modeled the future metapopulation dynamics of whitebark pine in Mt. Rainier National Park with a spatially explicit Lefkovitch stage-based model using life history data collected from the park (DelPrato 1999) and from the Greater Yellowstone area. The model allowed incorporation of demographic stochasticity and environmental fluctuations. Parameters were modified to show how the population trajectory changed with stochasticity in blister rust infection rates, fire frequency, density dependence, dispersal rate and distance, increased blister rust resistance, and management activities including pruning and plantings. All simulations predicted population declines except for those including the introduction of genetically resistant stock through plantings. Without any management intervention, the 150-year simulation predicts a greater than 65 percent chance of whitebark pine extinction in the park and a 95 percent probability of populations falling below 500 individuals at any time.

For whitebark pine in Crater Lake National Park, Murray and Rasmussen (2000, 2003) predicted an overall decline of 0.4 percent for mature trees annually, based on estimates of 0.7 percent annual loss and an optimistic estimate of 0.3 percent recruitment. This would lead to a 20 percent reduction in the number of whitebark pines in the park within 50 years, which would represent a halving of the historical abundance of whitebark pine in the area.

In the absence of any other formal studies of whitebark pine population dynamics, the life history data collected during stand health assessments may hint at regeneration potential and population trends in other parts of the Pacific Northwest. Several studies noted the size class distribution of whitebark pine encountered in sampled stands (Hadfield et al. 1996; Goheen et al. 2002; Shoal and Aubry 2004; Doede, unpublished data). Although the age structure of whitebark pine was extremely variable among transects within each study, in three of these studies the majority of trees encountered were in the sapling size class (diameter at breast height [dbh] of 5 inches [12.7 cm] or less) (Goheen et al. 2002; Shoal and Aubry 2004; Doede, unpublished data). Olympic National Forest stands had the most dramatic age structuring, with 89 percent saplings and only 9 percent poles (5 to 9 inches [21.7 to 22.9cm] dbh) and 3 percent mature trees (over 9 inches [22.9cm] dbh) (Shoal and Aubry 2004).

Whitebark pine is known for its masting pattern of cone production, with synchronous abundant cone production in some years (“mast years”) and very little cone production in others (“fail years”). There is some evidence that the frequency of abundant cone crops may vary regionally; reports of 4 consecutive years of moderate to heavy crops in the Sierras contrast with the 3- to 4-year intervals between cone crops in the Greater Yellowstone Area (McCaughey and Tomback 2001). There are no data chronicling cone crop sizes over time in the Pacific Northwest; however, some stand assessments included observations on cone crops. The year 2003 was a good cone crop year for whitebark pine in Washington and Oregon. Shoal and Aubry (2004) note that 14 percent of all clumps observed contained mature cones. On the Mt. Hood National Forest that same year, all sites surveyed had evidence of some cone production, and at four sites, cones were present on more than 30 percent of the live stems (Doede, unpublished data). Cone crops were patchy and moderate across the region in 2005, and it appears that there will be a similar cone crop in 2006.

Genetic variation in Washington and Oregon

Successful management for the conservation and restoration of whitebark pine will depend on a good understanding of the patterns of genetic variation for phenotypic adaptive traits such as growth rate or resistance to white pine blister rust (Dekker-Robertson and Bruederle 2001). The common garden studies required to assess adaptive genetic variation take many years to complete, and one such study is currently underway that includes Pacific Northwest populations (Bower 2003). In the meantime, the immediacy of the threat to whitebark pine demands the use of more readily available information (Hoff et al. 2001). Biochemical data from enzymes (isozymes) or DNA markers that can be obtained in the laboratory provide insight into patterns of selectively neutral genetic variation, levels of inbreeding, and patterns of gene flow that can inform the development of preliminary gene conservation guidelines (Dekker-Robertson and Bruederle 2001).

Four studies examining range-wide variation in genetic markers have included samples from Washington and/or Oregon. Jorgensen and Hamrick (1997) characterized patterns of genetic variation of isozymes within and among 30 whitebark pine populations sampled from across the species range. Of these 30 sites, 3 were in Washington (Washington Pass, Mt. Rainier National Park, and Mt. Adams) and 3 were in Oregon (Mt. Hood, Bachelor Peak, and Crater Lake National Park). Richardson et al. (2002a, 2002b) analyzed DNA markers to examine population genetic structure and biogeographic patterns in 41 populations from across the range. These studies included 8 sample sites in Washington (Chinook Pass, Washington Pass, Fox Mtn. Pass, Rock Mtn., Mission Ridge, Manastash Ridge, Ravens Roost, and Potato Hill) and 4 sites in Oregon (Brown Mtn., Crater Lake, Harriman and Pelican). Isozyme analysis of 1 of the 17 populations sampled in Krakowski et al. (2003) was from northern Washington on the eastern slope of the Cascades. The following discussion highlights the findings from these studies that are relevant to whitebark pine in Washington and Oregon.

Genetic diversity

Genetic diversity is measured by several common statistics. ***Expected heterozygosity*** *estimates the fraction of individuals that are heterozygous at any random locus. Other measures of diversity include the* ***percent of polymorphic loci*** *(the percent of genetic markers that have more than one allele) and the* ***mean number of alleles per polymorphic locus****.*

Measures of genetic diversity differed markedly among the studies and depended on the type of genetic marker used (isozyme or DNA) and on the statistic reported. Using isozymes, Jorgensen and Hamrick (1997) found low expected heterozygosity both within populations (ranging from 0.07 to 0.109 in Washington and Oregon populations) and within the species as a whole (0.102). These authors reported that whitebark pine has very low genetic diversity compared to other pines, including other stone pines, at both the population and the species level. In contrast, isozyme data in Krakowski et al. (2003) yielded expected heterozygosity of 0.257 in the species overall and 0.260 in one population sampled from Washington. These measures fall midrange among reported values for pine species (Jorgensen and Hamrick 1997, Bruederle et al. 2001). Using chloroplast (cp)DNA, Richardson et al. (2002a) found very high values for gene diversity, the haploid equivalent of expected heterozygosity. Gene diversity was 0.928 for the northern Cascades and 0.915 for southern Oregon.

Although Jorgensen and Hamrick (1997) found overall genetic diversity was low as measured by expected heterozygosity, the incidence of rare alleles (rare genetic variants) in the species overall appeared to be high, resulting in a high proportion of polymorphic loci (85 percent) and a large number of alleles per polymorphic locus (Jorgensen and Hamrick 1997). Because these rare alleles are distributed among populations rather than within them, gene conservation efforts would require widespread sampling within and among populations in a variety of locations to capture a substantial portion of the allelic diversity (Jorgensen and Hamrick 1997). Because blister rust resistance is likely to be rare, conserving this allelic diversity may be crucial to whitebark pine's ability to evolve in response to the evolving pathogen, white pine blister rust fungus (Hoff et al. 1994, Jorgensen and Hamrick 1997).

Genetic differentiation

Estimates for genetic differentiation among populations were low to moderate in all studies from the region, ranging from G_{ST} = 0.034 (Jorgensen and Hamrick 1997) to G_{ST} = 0.061 (Krakowski et al. 2003) and suggesting that most genetic variation in whitebark pine is found within populations. These measures of genetic differentiation are low compared to other pine species, but especially low for a species with a fragmented distribution. On average, individual populations maintained 97 percent of the genetic variation found within the whole species (Jorgensen and Hamrick 1997). Estimates of the numbers of migrants per generation in this study suggest that gene flow should overcome the diversifying effects of genetic drift.

G_{ST} estimates the proportion (between 0 and 1) of genetic variation that results from differences among populations as opposed to differences within populations.

Inbreeding

Significant levels of inbreeding were documented in whitebark pine (Jorgensen and Hamrick 1997, Krakowski et al. 2003), which may increase the susceptibility of populations to blister rust. Krakowski et al. (2003) infer a broad geographic relationship between blister rust mortality and levels of inbreeding. They theorize that surviving populations in areas hard hit by the disease exhibit lower inbreeding because inbred individuals may have been more sensitive to the disease and thus may have been selected out of the populations.

Regional patterns of genetic variation

Evidence of slight genetic divergence between the eastern and western regions of whitebark pine's range was revealed using both isozymes (Jorgensen and Hamrick 1997) and mitochondrial DNA (mtDNA) (Richardson et al. 2002a, 2002b).

Jorgensen and Hamrick (1997) found that whitebark pine in the Cascades had lower within-population genetic diversity and greater differences between populations than it did in the Rocky Mountains and Sierra Nevada resulting from either smaller refugia during the last glaciation or from a history of smaller and more isolated populations. Whitebark pine is restricted to a narrower climatic and elevational band in the Cascades, and these results support the claim that these populations are more isolated from each other.

A notable exception to the overall pattern of lower within-population genetic diversity in the Cascades was found in a population from Mt. Rainier. This population had measures of diversity more similar to measures from Rocky Mountain and Sierra Nevada populations, and it differed from all other populations rangewide in the relative proportions of the gene variants it contained.

Distinct regionality was also found in the distribution of mitochondrial DNA (mtDNA) variants range-wide, with an abrupt contact zone near Mt. Rainier (Richardson et al. 2002a, 2002b). Mitochondrial DNA variants in Yellowstone and the Sierra Nevada are thought to have remained separated from each other during the last glacial period. Subsequent recolonization of whitebark pine habitat to the north and west may have rejoined these two previously isolated regions in a 100-km band from Chinook Pass, Washington, to Snoqualmie Pass, Washington (Richardson et al. 2002a).

However, in contrast to the regionality of mtDNA variation, patterns of cpDNA variation showed low genetic differentiation (Richardson et al. 2002a). Because cpDNA is inherited only through pollen in the Pinaceae, comparisons between patterns of variation in mtDNA and cpDNA can distinguish between gene flow resulting from seed dispersal and that resulting from wind pollination. Richardson et al. (2002a) suggested that although gene flow through seed dispersal was limited between regions, substantial historical levels of gene flow through wind pollination linked populations in the Cascades to populations in the eastern part of the range in northern and central Idaho.

A smaller scale study within the contact zone in the Washington Cascades assessed patterns of nutcracker seed dispersal within and among populations (Richardson et al 2002b). Patterns of mtDNA variation suggested that nutcrackers distribute genes essentially randomly within populations, in keeping with previous studies (Furnier et al. 1987, Rogers et al. 1999), but rarely transfer genes between distant populations. In particular, Snoqualmie Pass appears to be a barrier to gene flow through nutcracker seed dispersal. One mtDNA variant was found exclusively to the south of the pass, and the other was found almost entirely to the north, with only two cases of dispersal events to the south at Manastash Ridge and Mission Ridge. Because Clark's nutcracker only rarely disperses seed farther than 12 km (Tomback 2001), the 30-km gap in subalpine habitat in the relatively low elevations at Snoqualmie Pass may have blocked north–south seed dispersal in this area. However, because cpDNA data showed high levels of gene flow via pollen here, Richardson et al. (2002b) conclude that the nutcracker's primary role is as an agent of regeneration, while wind pollination accounts for the majority of gene flow among populations.

A study is currently underway to describe patterns of genetic diversity in whitebark pine in Washington State. The study area includes all national parks and national forests in the state. Isozyme, cpDNA, and mtDNA analysis will be used. The analysis is being conducted by the National Forest Genetics Electrophoresis Laboratory under a partnership among the National Park Service, National Forest Service, and the Rocky Mountain Research Station (Rochefort et al., in preparation).

Fire history and disturbance regimes

The effects of fire and other disturbances on whitebark pine establishment and persistence can vary with changing ecological conditions faced by the tree (Arno 2001). For example, while fire may play a crucial role in providing opportunities for whitebark pine to escape competition from late seral species in lower elevations and wetter, more productive sites, it can have the opposite effect on dry, wind-exposed sites where regeneration after a severe fire may require several decades (Arno and Hoff 1990). Therefore the optimal fire regime for whitebark pine could be unique in the maritime climate of the Pacific Northwest and may vary among ecoregions with associated differences in plant communities.

Siderius and Murray (2004) offer the only documentation of fire regimes in whitebark pine stands in the Pacific Northwest. In a study of fire frequency and severity at two sites in the Washington Cascades (Stormy Mountain on the Wenatchee National Forest and Crystal Lake in Mt. Rainier National Park) they found site-specific variation in fire regimes. Stormy Mountain exhibited a low severity fire regime with fire scar intervals averaging 40 years (range 18 to 67 years), while the Crystal Lake site displayed both low and high severity fire, and was estimated to burn every 70 to 90 years. The authors suggest that factors such as local climate, aspect, slope, fuel contagion, and stand structure could drive this variation. Specifically the frequent pattern of low severity fires at Stormy Mountain may be partially explained by the prevalence of grasses at the site.

This research is part of an ongoing larger study documenting fire history on 55 sites in the Cascade Range (Murray, personal communication, 2005). Preliminary analysis of scar and core sampling data from these sites show considerable variation in the severity and frequency of fire in whitebark pine ecosystems in the region. However, the widespread occurrence of fire throughout the sampled area (88 percent of stands encountered had evidence of fire) points to the significance of fire as a disturbance agent in the northwest. Fire intervals at these sites averaged 67 years and varied between 9 and 314 years.

The future of whitebark pine in the Pacific Northwest

Just as in other portions of its range, the long-term survival of whitebark pine and whitebark pine ecosystems in Washington and Oregon is likely to depend on active conservation and restoration efforts. Achieving a thorough understanding of the ecology of whitebark pine in the Pacific Northwest is an important prerequisite for developing management strategies appropriate to the region. Additional ongoing restoration efforts supported by the Pacific Northwest Albicaulis Project include cone collections, blister rust resistance studies, studies of genetic variation in whitebark pine across the region, and studies of Clark’s nutcracker ecology and whitebark pine regeneration.

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Appendix A: Detailed summaries of whitebark pine stand health assessments

This appendix summarizes studies that have been conducted on public lands in each of Bailey’s (1995) ecoregions present in Washington and Oregon (fig. 2).

Okanogan Highlands Ecoregion

High-elevation habitat supporting whitebark pine in the Okanogan Highlands ecoregion occurs on the Colville National Forest and the eastern portion of the Okanogan National Forest.

Colville National Forest

Hoff conducted a transect survey on Salmo Mountain in 1992 and found that 75 percent of seedlings observed were infected with blister rust (Kendall 1994b). No methods or sample sizes were reported. Health assessments were conducted in four whitebark pine stands (one transect per stand) on the Colville National Forest in 2004 (Shoal and Aubry, unpublished data). The field sampling protocol was a modified version of the methods advocated by the Whitebark Pine Ecosystem Foundation (Tomback et al. 2004). Transects were 33 feet (10 m) wide. Transect length varied depending on the site, with a minimum length of 164 feet (50 m) and the maximum length depending on the distance it took to encounter 50 whitebark pine stems, at least 30 of which were living. Analysis of the data for this paper showed that on average, 24 percent of whitebark pine stems within each stand were dead (range 20–33 percent), and 33 percent of the living stems within each stand were infected with blister rust (range 23–44 percent).

Eastern Cascades Ecoregion

Whitebark pine is distributed throughout all national forests, national parks, and Indian reservation lands that occur in the Eastern Cascades Ecoregion.

Okanogan National Forest

A single whitebark pine stand at Trinity Mountain on the Okanogan National Forest was surveyed in 1996 (Hadfield et al. 1996). The researchers’ method was to examine all whitebark pines within 5–10 feet (1.5–3 m) of both sides of a compass line transect. Transect length and width varied with tree densities, but at least 50 trees were examined on each transect. Twenty-seven percent of whitebark pine stems were infected with blister rust (table 1 and fig. 4), but this percentage may include dead as well as living trees (Hadfield, personal communication, 2005). Mature trees had a higher incidence of infection (44 percent) than poles (38 percent), saplings (16 percent), or seedlings (9 percent). Two percent mortality was also recorded at this site, although cause of death was not determined.

Twelve additional stands were assessed on the Okanogan National Forest between 2003 and 2005 (Shoal and Aubry 2004; Shoal and Aubry, unpublished data). Survey methods differed slightly among years.

In the eight stands surveyed in 2003, the protocol was based on Smith and Hoffman (1998). Transects were 15 feet (4.6 m) wide and their length varied depending on the distance it took to encounter 50 clumps of whitebark pine, of which 30 or more contained at least one living stem. Clumps were the unit of measurement in this survey because individual stems within a multi-stem clump are likely to be close relatives (Shoal and

Aubry 2004). Across all four forests included in this study (see discussions under Wenatchee, Mt. Baker-Snoqualmie, and Olympic national forests), clump size averaged 2.5 stems per clump, with 44 percent of clumps consisting of a single stem and 20 percent consisting of 2 stems. Pooling all transects together, the overall mortality was 16 percent of all stems observed, but cause of death was difficult to determine. Blister rust was present on all transects conducted on the Okanogan National Forest in 2003. The prevalence of infection per transect ranged from 20 percent to 77 percent, and pooling all transects together yielded an overall infection rate of 45 percent. These percentages were calculated as the proportion of clumps containing at least one infected living tree among all clumps encountered (both living and dead). Reanalysis of the data for this paper showed the mean percent of living clumps infected per stand was 48 percent (range 21–84 percent); the average mortality per stand calculated for this review was the same value as that reported in the original analysis: 16 percent (range 6–42 percent). The severity of infection was scored in 2003 with a score from 0 (no infection) to 4 (bole infected). The average severity of infection across all surveys on the Okanogan National Forest was 2.9 (range 2.3–3.5), where scores of 3 and 4 are considered to be lethal to the tree. Blister rust infection rates were noted separately for three size classes, but no pattern of differential susceptibility to infection was observed.

Survey protocols in 2004 and 2005 (Shoal and Aubry, unpublished data) followed the method described above for the Colville National Forest. Analysis of the data for this paper showed that on average, 33 percent of whitebark pine stems within a stand were dead (range 14–45 percent), and 52 percent of the living stems within each stand were infected with blister rust (range 31–73 percent). Results for two stands surveyed in the Pasayten Wilderness in 2005 are currently being analyzed.

Wenatchee National Forest

Bedwell and Childs (1943) provide the earliest documentation of blister rust infection in whitebark pine stands on the Wenatchee National Forest at Hyas Lake, just east of Snoqualmie Pass. Of nine living whitebark pine trees observed, eight (89 percent) were infected with blister rust.

Hadfield et al. (1996) surveyed three stands on the Wenatchee National Forest in 1996. Their transect methods are described above under the Okanogan National Forest. Pooling observations from all three transects, they found 12 percent mortality, although cause of death was undetermined. Sixteen percent of the 257 stems tallied were infected with blister rust, but again this percentage may include dead as well as living trees (Hadfield, personal communication, 2005). Reanalysis of the data for this paper did not affect the estimate of mortality—on average, 12 percent of whitebark pine stems within each stand were dead (range 8–14 percent); however, the estimate of blister rust prevalence was higher—19 percent of the stems (possibly including dead stems) within each stand were infected with blister rust (range 16–21 percent). Pooling data across all three transects, Hadfield et al. (1996) reported that infection rates were similar in seedlings (18 percent), saplings (19 percent), poles (20 percent), and mature trees (21 percent).

Additional stands were surveyed on the Wenatchee National Forest in 2002 and 2005 (Shoal and Aubry 2004; Shoal and Aubry, unpublished data). Sampling methods varied between years and are described above in the Okanogan and Colville National Forest sections. Data collected in 2005, including five stands from the Alpine Lakes Wilderness Area, are currently being analyzed. Blister rust was present on every transect but two in the earlier study (Shoal and Aubry 2004). Sixteen percent of all 980 living and dead whitebark pine clumps encountered across all transects were alive but infected with blister rust. Reanalysis of the raw data for this review increased the estimate only slightly: the mean percentage of living clumps infected per stand was 17 percent (range 0–67 percent). Mortality in the one transect where mortality was measured was 40 percent (Shoal and Aubry 2004). Blister rust infections were relatively severe on average, with a mean score of 2.9 out of a possible range of 0–4. The prevalence of blister rust varied widely by transect in this study, even among sites in close proximity to each other. The Wenatchee National Forest had a low incidence of infection relative to the other four national forests surveyed, but relatively high mortality (Shoal and Aubry 2004).

Yakama Indian Reservation

Hadfield et al. (1996) surveyed whitebark pine mortality on two transects on the Yakama Indian Reservation using the methods described in the Okanogan National Forest section. Twenty-three percent of 101 trees were infected with blister rust, but this percentage may include dead as well as living trees (Hadfield, personal communication, 2005). The average percentage of infected trees per stand revealed by reanalysis in this paper was 24 percent (range 21–28 percent) and mortality (cause of death not determined) averaged 7 percent (range 6–8 percent). Pooling the data from the two stands, saplings and poles had higher infection rates (36 percent and 54 percent respectively) than seedlings (0 percent) or mature trees (11 percent).

Mt. Hood National Forest

Although the Mt. Hood National Forest spans the eastern and western sides of the Cascade Crest, reports of rust infection and mortality rates are discussed in the Eastern Cascades section of this appendix because the majority of sites sampled occurred in the Eastern Cascades Ecoregion (Roantree, personal communication, 2005).

Bedwell and Childs (1943) provided the earliest reports of blister infection on the Mt. Hood National Forest. Of the 17 living trees sampled at each site, 94 percent were infected at Salmon River, 88 percent were infected at White River, and 100 percent were infected at Frog Lake Butte. These infection rates were much higher than more recent surveys in the area have documented, but this may result in part from the small sample sizes.

Assessments of whitebark pine health were conducted in 10 stands on the Mt. Hood National Forest in 2003 (Doede, unpublished data). Data were collected from one transect in each stand. Transects varied in width and length to allow surveyors to assess at least 50 whitebark pine clumps greater than 4.5 feet (1.4 m) tall, of which at least 30 contained at least one living tree. Blister rust infection data provided for the analysis in this paper were recorded on a per-clump basis, while mortality was recorded by the stem and by the clump. The average percentage of infected clumps per stand was 51 percent (range 23–90 percent) and the average mortality per stand was 40 percent (range 5–89 percent) (tables 1 and 2, figs. 4 and 5).

Warm Springs Indian Reservation

Bedwell and Childs (1943) documented that 71 percent of 17 living trees sampled at Mt. Wilson were infected with blister rust.

Deschutes National Forest

Five stands on the Deschutes National Forest were surveyed with nine transects in 2004 (Doede, unpublished data). Transects were 33 feet (10 m) wide, and their length varied from 164 feet (50 m) to whatever length was required to sample at least 50 whitebark pine clumps greater than 4.5 feet (1.4 m) tall, of which at least 30 contained one or more living trees. As in the surveys on the Mt. Hood, Willamette, and Gifford Pinchot national forests by the same author, blister rust infection data provided for the analysis in this paper were recorded on a per-clump basis, while mortality was recorded by the stem and by the clump. The average percentage of infected clumps per stand was 29 percent (range 16–60 percent) and the average mortality per stand was 33 percent (range 19–51 percent).

Umpqua National Forest

Goheen et al. (2002) surveyed white pine blister rust along the Pacific Crest National Scenic Trail on the eastern edge of Umpqua National Forest in 1998. The survey method was a combination of plots and transects. Whitebark pine trees were examined in six 0.02-ha and six overlapping variable-radius plots for each of 21 transects. Additional plots were surveyed for other plant community data. White pine blister rust was present in all transects with whitebark pine. Pooling the data for all transects showed 46 percent of all living and dead whitebark pine trees encountered were live but infected with blister rust. The prevalence of infection for each transect was reported as the number of infected trees per hectare. Rust prevalence varied from transect to transect, ranging from 0 to 100 percent. Susceptibility to blister rust infection did not appear to vary with size class, with two exceptions: very few seedlings less than 2 feet (0.6 m) tall were infected, and trees with greater than 20-inch (50-cm) diameter at breast height (dbh) had no infection. Ten percent of all whitebark pine were dead, and two-thirds of this mortality was attributed to blister rust. Severity of infection was scored in a way that is directly comparable to results in Shoal and Aubry (2004). Blister rust infections, when they occurred, were severe: 92 percent of infected whitebark pines had bole cankers or cankers within 6 inches (15 cm) of the bole. These infections would be assigned scores of 3 and 4, considered lethal in Shoal and Aubry (2004). The numbers of infected and uninfected trees per stand were not available for reanalysis, so the results reported in tables 1 and 2 are from the original source.

Crater Lake National Park

Kendall (1994a, b) reported that in a 1992 trail transect in Crater Lake National Park, Ray Hoff observed 47 percent of whitebark pine trees with blister rust infections. Five percent were dead of unknown cause. Sample size, transect length, and condition of infected trees (living or dead) were not reported.

Murray and Rasmussen (2000, 2003) conducted the first systematic survey for blister rust infection at Crater Lake National Park. They sampled 24 transects in a total of 16 stands. Transects had variable widths and lengths; the first 50 live and dead trees along each transect were assessed for damaging agents. Pooling over all transects, blister rust occurred on 8 percent of all trees surveyed (including dead trees), ranging from 0 to 20 percent infection per transect. Reanalysis of raw data from 22 of the 24 transects shows the mean percent of living trees infected per stand was 11 percent (range 0–27 percent), and the average mortality per stand was 12 percent (range 4–29 percent). The original report documented blister rust on all size classes: 8 percent of mature trees greater than 9.8 in (25cm) dbh were infected, 12 percent of trees 0.04–9.5 in (0.1–24 cm) dbh were infected, and 3 percent of saplings shorter than breast height were infected. Eleven of the 24 transects had *Ribes* species present. These transects had a significantly greater incidence of blister rust (12 percent) than did transects without *Ribes* (4 percent).

Western Cascades Ecoregion

Whitebark pine occurs only occasionally on the western slopes of the Cascades, typically on dry southwest-facing slopes (Arno and Hoff 1990). Although stands are sparsely distributed in this ecoregion, they occur from north to south in North Cascades National Park, the Mt. Baker-Snoqualmie National Forest, Mt. Rainier National Park, and the Gifford Pinchot, Mt. Hood, and Willamette and Umpqua national forests (fig. 2).

North Cascades National Park

North Cascades National Park spans the Eastern and Western Cascades ecoregions but falls mostly within the Western Cascades Ecoregion (fig. 2), so it is listed here for the purposes of this discussion (tables 1 and 2, figs. 4 and 5). The prevalence of white pine blister rust on whitebark pine was quantified in the park between 1994 and 1999 (Rochefort 1995a, 1995b; Rochefort, personal communication, 2004). Incidences of blister rust and percent mortality were recorded in 13 plots of 0.1 acre (0.04 ha) within 10 whitebark pine stands in the park. The percentage of trees infected with blister rust was noted for mature trees (greater than1 in. dbh) and saplings (less than 1 in. dbh) separately. Data for mature trees only were analyzed here. On average, 26 percent of mature whitebark pine stems within a stand were dead (range 3–92 percent), and 55 percent of the living stems within a stand were infected with blister rust (range 0–74 percent).

Mt.Baker-Snoqualmie National Forest

Surveys in a limited area near Crystal Mountain northeast of Mt. Rainier provide the only documentation of blister rust infection rates on whitebark pine on the Mt. Baker-Snoqualmie National Forest (Shoal and Aubry 2004). Sampling methods followed Smith and Hoffman (1998) and are described in the section on the Okanogan National Forest. Pooling all data collected from the three stands revealed that 61 percent of all living and dead clumps surveyed were alive but infected with blister rust, while mortality of individual stems was 41 percent. Reanalysis of the raw data for this review shows that on average, 41 percent of whitebark pine stems within a stand were dead (range 26–53 percent), and 76 percent of the living clumps per stand were infected with blister rust (range 65–84 percent). Scores for the severity of infection (0–4) were also relatively high, with the average infections being lethal (3.4 for all transects pooled). The authors reported that whitebark pine stands in the Mt. Baker-Snoqualmie National Forest had the highest incidence of blister rust infection, the most severe infections, and the highest mortality compared to the other three forests they surveyed (Shoal and Aubry 2004).

Mt. Rainier National Park

In 1935, a vegetation survey in Mt. Rainier National Park identified 67 whitebark pine stands and classified them into five community types: subalpine parkland, whitebark pinedominated, Alaska yellow-cedar (*Chamaecyparis nootkatensis*) dominated, subalpine fir (*Abies lasiocarpa*) dominated, and mountain hemlock (*Tsuga mertensiana*) dominated (Rochefort 1995a, 1995). Nineteen of these stands were assessed for mortality and blister rust infection rates between 1994 and 1999 (Rochefort, personal communication, 2004). Surveys were conducted in 0.1-acre (0.04-ha) plots, and 1–12 plots were sampled in each stand. The percentage of trees infected with blister rust was noted for mature trees (greater than 1 in. dbh) and saplings (less than 1 in. dbh) separately. A total of 2,409 mature trees and saplings have been examined, which is the largest sample size of any study in Washington and Oregon to date. Preliminary findings after 1 year showed that 22 percent of all living and dead mature trees were alive but infected with rust in the subalpine fir dominated stands, while 20 percent were infected in subalpine parkland stands, 15 percent in mountain hemlock dominated stands, and 8 percent in whitebark pine dominated stands (Rochefort 1995b). With permission of the author, raw data from the 1994–1999 period were analyzed for this report. On average, 41 percent of whitebark pine stems within each stand were dead (range 13–84 percent), and 23 percent of the living stems within each stand were infected with blister rust (range 0–55 percent).

Gynn and Chapman (cited in Hoff and Hagle 1990) reported that 55 percent of 602 whitebark pine trees surveyed and 52 percent of 297 trees surveyed in the park in 1951 and 1952 respectively were infected with blister rust. The original source was not available for examination for this study, so it is not clear whether the percentages and sample sizes include dead trees or only living trees. Summary of these results using the ratio of means procedure yielded an average of 54 percent infected trees per stand (table 1).

Kendall (1994a, 1994b) reported that Hoff found 95 percent of all mature whitebark pine at Sunrise Ridge were infected with rust, and 25 percent were dead of unknown causes. Sample size was not reported. This incidence is dramatically higher than that reported by Rochefort's systematic survey. This disparity could be caused by higher local infection near Sunrise, a difference in methodology, or differences in sample sizes.

Gifford Pinchot National Forest

Seven stands on the Gifford Pinchot National Forest were assessed in 2004 (Doede, unpublished data). Sampling methods were the same as those described in the Deschutes National Forest study. Blister rust infection data provided for the analysis in this paper were recorded on a per-clump basis, while mortality was recorded by the stem and by the clump. On average, 25 percent of living clumps within a stand were infected (range 8–57 percent) and 40 percent of stems per stand were dead (range 0–55).

Willamette National Forest

Bedwell and Childs (1943) noted that blister rust was observed as far south as Mt. Jefferson by 1943, but the authors did not provide data on the prevalence of infection. Surveys conducted in 2004 included three stands on the Willamette National Forest. Methods were identical to those described for the Deschutes National Forest (Doede, unpublished data). Blister rust infection data provided for the analysis in this paper were recorded on a per-clump basis, while mortality was recorded by the stem and by the clump. On average, the percent of living clumps infected per stand was 77 percent (range 47–100), and mean percent mortality per stand was 38 percent (range 31–49).

Coast Range Ecoregion

Whitebark pine is restricted to a few isolated populations in the rain-shadow of the Olympic Mountains on the northeast corner of the Olympic Peninsula in Washington (fig 2).

Olympic National Forest

Although 92 percent of living whitebark pine trees surveyed at Marmot Pass in the 1930s were blister-rust-infected (Bedwell and Childs 1943), recent assessments have shown much lower infection rates. Pooled data from five stands sampled in the Buckhorn Wilderness in 2002 and 2003 showed that 21 percent of living and dead clumps sampled were alive but infected with blister rust, while 25 percent of all individual stems were dead (Shoal and Aubry 2004). Reanalysis for this paper yielded almost identical estimates: on average, 22 percent of living clumps were infected (range 11–49 percent) and the mean percent mortality per stand was 25 percent (range 8–46 percent). The average infection severity score reported in the original source was 3.2 (a score of 3 or higher is considered potentially lethal).

Olympic National Park

Three whitebark pine stands in Olympic National Park were surveyed in 2004 (Acker and Shoal, unpublished data). The field sampling protocol was identical to that in Shoal and Aubry (2004). Initial analysis of the data for this report showed that on average, 21 percent of whitebark pine stems within each stand were dead (range 2–28 percent), and 14 percent of the living stems within each stand were infected with blister rust (range 4–32 percent).

Blue Mountains Ecoregion

The Blue and Wallowa mountains contain isolated populations of whitebark pine outside the main distribution of the species (Arno and Hoff 1990). The tree occurs in small scattered populations in the Vinegar Hill area on Umatilla National Forest, in the Wallowa and Elkhorn mountains on the Wallowa-Whitman National Forest, and in the Strawberry mountains on the Malheur National Forest (Erickson, personal communication).

Umatilla and Malheur National Forests

Stand assessment data were collected in 2002–2003 from 153 plots spread out over 30 stands in the Vinegar Hill area on the Umatilla and Malheur national forests (Erickson, unpublished data). The sampling effort averaged six plots per stand (range 3–18). Within each stand, circular plots were arrayed in a randomly placed grid with their centers separated by a minimum of 66 feet. All living and dead whitebark pine trees with a dbh greater than 4.0 in (10.2 cm) were sampled within 0.1-acre (0.04-ha) plots. Smaller 0.05-acre (0.02-ha) plots were used to sample whitebark pine seedlings. With permission of the author (Erickson, personal communication, 2005), the average percentage of affected trees per stand was calculated here using the ratio of means procedure (Cochran 1977). On average, 24 percent of whitebark pine stems within each stand were dead (range 0–68 percent) and 64 percent of the living stems within each stand were infected with blister rust (range 0–100 percent).

Malheur National Forest

The Malheur National Forest has submitted a proposal to conduct surveys in the Strawberry Mountains (Erickson, personal communication, 2005).

Wallowa-Whitman National Forest

Stand assessments completed in the Wallowa and Elkhorn Mountains in 2005 are currently being analyzed (Erickson, personal communication, 2005).