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WHITEBARK PINE RESTORATION STRATEGY FOR THE PACIFIC NORTHWEST REGION

2009-2013



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COVER PHOTOS

Main photo; Robin Shoal, U.S. Forest Service; small photos—Clark's nutcracker obtaining seed from whitebark pine cone, Teresa Lorenz, U.S. Forest Service; four cones, Robin Shoal, U.S. Forest Service; krummholtz, Robin Shoal, U.S. Forest Service; grizzly cubs, National Park Service.

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FOR THE PACIFIC NORTHWEST REGION 2009–2013

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OUR GOAL

Restore and conserve a network of viable populations of whitebark pine and associated species across the Pacific Northwest

- Restore degraded habitat
- **Protect** genetic resources through gene conservation
- **Increase** blister rust resistance in whitebark pine populations
- Evaluate the health and status of whitebark pine stands where lacking
- **Increase** our understanding of the threats to whitebark pine and develop practical and effective restoration techniques.

PRIORITY ACTIONS

Implement a comprehensive 5-year restoration plan to:

- A. Restore areas where whitebark pine habitat has been affected by fire, mountain pine beetle, or white pine blister rust by planting seed or seedlings, thinning competing trees, or pruning tree infected limbs.
- **B.** Collect whitebark pine seed samples across the Pacific Northwest and **protect** in long-term storage.
- C. Increase levels of genetic resistance to blister rust infection by in whitebark pine populations through tree selection, resistance screening, and wise use of seed from resistant trees.
- **D.** Evaluate units where health, stand condition, and restoration needs are unknown.
- E. Work collaboratively with research scientists and land managers in other agencies to **increase** understanding of the complex and synergistic impacts of blister rust, fire, mountain pine beetle and climate change on present and future health and distribution of whitebark pine plant communities

WHY WE ARE CONCERNED

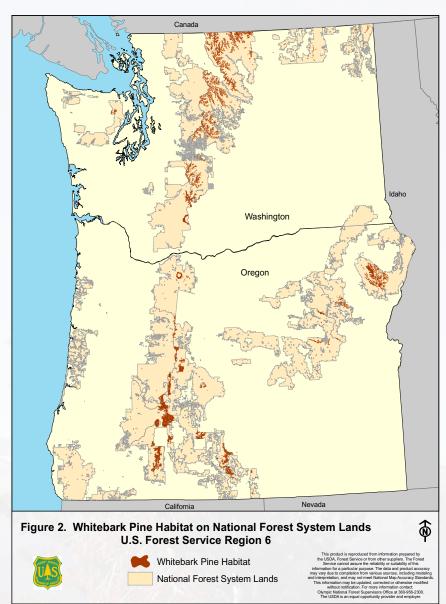
Whitebark pine has been widely described as a "keystone" species in high-elevation forests (Tomback et al. 2001, Schwandt 2006): an important ecosystem component that influences the success of other organisms. It plays a vital role in first colonizing areas disturbed by fire or landslides, stabilizing the soil, moderating snow melt, and providing the cover that allows regeneration of other tree species.

The future of whitebark pine in Oregon and Washington as well as throughout its range is of serious concern because of the species' acute vulnerability to infection by the non-native fungus *Cronartium ribicola* (which causes white pine blister rust), its high susceptibility to infestation by mountain pine beetle (*Dendroctonus ponderosae*), its risk of being destroyed in large and intense wildfires, and the likelihood of its being replaced in some subalpine mixed conifer forests by more shade-tolerant tree species, a trend that is exacerbated by fire exclusion. There are also significant concerns about the impacts of climate change, particularly warming, on this high-elevation, cold-adapted species.

Proactive conservation and restoration are critical to prevent the permanent loss of whitebark pine habitat throughout much of its range in the Pacific Northwest.

PORTRAIT OF WHITEBARK PINE

Whitebark pine is a medium-sized tree with characteristics adapted for survival in high mountains (Arno and Hoff 1990). In Oregon and Washington, it occurs mainly at elevations of 1,600 m to 2,800 m. Multiple stems representing a single tree or several very closely associated trees are common in open stands. At the high end of its elevation range on exposed sites where hurricane-force winds are common in winter, it assumes a stunted, krummholz form. Even in less inhospitable locations, whitebark pine frequently exhibits a picturesque, windswept appearance. Whitebark pine habitat is characterized by severe conditions (Arno and Hoff 1990), including: short, cool, often droughty summers; growing seasons of fewer than 110 days; and frosts and even snow showers during summer months.



Whitebark pine populations tend to be scattered and spotty because of the often discontinuous distribution of favorable habitat on high mountain peaks and ridges.



Robin Shoal, USFS

Individual populations are of widely varying sizes, with some being quite small. Along the north–south running Cascades where the largest numbers of whitebark pine populations in the Pacific Northwest occur, the drier regions east of the Cascade Crest commonly have more suitable habitat than areas farther west (Ward et al. 2006b). Some Pacific Northwest whitebark pine populations, notably those in the Olympic and Blue Mountains, are widely separated from any other populations, and the populations in northeastern Washington are closer to the Rocky Mountain portion of the species' range than they are to the Cascades.

At the high end of its elevation range and on exposed or dry sites where conditions are too extreme for other tree species, whitebark pine may grow virtually alone and be the climax species. At lower elevations where more hospitable weather conditions prevail and whitebark pine is a component of subalpine mixed conifer forests, it is frequently the pioneer species that grows first on a site following disturbance and provides the cover that eventually allows more shade-tolerant tree species to become established. In the absence of additional disturbance, whitebark pine may be out-competed and replaced over time in such subalpine mixed stands by the more shade-tolerant true firs, spruces, and hemlocks.

Most whitebark pine habitat in Washington and Oregon occurs on federally administered land, and 81 percent is on lands administered by the Forest Service, Region 6. Sixty percent of the known occupied whitebark pine habitat on National Forest System land in the Pacific Northwest occurs in congressionally designated wilderness areas.

Seed dissemination by whitebark pine is unique among American pines. The species' large, wingless seeds are rarely if ever spread by wind or gravity. Instead whitebark pine seeds are mostly released from cones and disseminated by a bird species, the Clark's nuteracker (*Nucifraga columbiana*).

Numerous seeds buried in soil caches but not reclaimed by nutcrackers germinate, usually after two or more winters, and grow—resulting in successful whitebark pine regeneration, commonly found in small clumps. Using molecular markers, it has been determined that often the stems in these clumps represent more than one genetically distinct individual, with each one arising from a different seed.



Robin Shoal, USFS



el Murray, NP

Levels of genetic diversity in whitebark pine are comparable to other stone pine species; however, whitebark pine appears to have lower levels of genetic differences among stands than wind-dispersed pines do. While genetic analysis using molecular markers have shown low levels of genetic differentiation, studies using measured traits generally have found considerably more genetic variation and moderate to

high levels of population differentiation. The traits studied include cold injury, blister rust resistance, growth, and phenology. Winter temperature appears to be an important climatic determinant driving adaptation of populations to their local environment, and combined with data on population differentiation, has been used to determine guidelines for movement of seed for restoration or reforestation efforts.

WHITEBARK PINE AND WILDLIFE

Although among wildlife species only the Clark's nutcracker plays an important part in whitebark pine seed dissemination, many other wildlife species of high-elevation ecosystems depend to varying degrees on whitebark pine seeds as food resources (Lanner 1996). Other birds known to feed on whitebark pine seeds include jays, ravens, grosbeaks, chickadees, and nuthatches. Mammals include mice, chipmunks, squirrels, and bears. Two species of squirrel, the red squirrel (*Tamiasciurus hudsonicus*) and the Douglas squirrel (*T.* douglasii), in particular, harvest large numbers of whitebark pine cones in good seed years and store them in midden piles for winter food (Lanner 1996, Mattson et al. 2001). Black bears (*Ursis americana*) and grizzly bears (*U. arctos*) harvest whitebark pine cones themselves but more commonly raid squirrel middens to take advantage of the concentrated, high-quality food represented by the pine seeds in them. A plentiful supply of whitebark pine seeds in squirrel middens has been shown to



National Park Service

contribute substantially to the success of bear populations and also to reduce the amount of conflict between humans and grizzly bears (Mattson et al. 1992; Mattson et al. 2001). In northeastern Washington, the grizzly bear is a threatened species, so its welfare as it relates to whitebark pine is of considerable management importance.

THE FOUR THREATS TO WHITEBARK PINE

The major threats to whitebark pine in the Pacific Northwest are white pine blister rust, mountain pine beetle, fire (both too much and not enough in different situations), and large-scale climate change. All have been influenced or directly caused by human activities.

White Pine Blister Rust

The pathogenic fungus Cronartium ribicola, which causes white pine blister rust, is native to eastern Asia. The pathogen was first recognized in 1921 in British Columbia, by which time it had already spread into adjacent five-needle pine populations. Since its introduction, the pathogen has caused unprecedented decline and mortality of susceptible hosts in Oregon and Washington as well as other parts of the West. C. ribicola has a complex life cycle involving five spore types and requiring both pine and alternate hosts for its successful completion (Boyce 1961); alternate hosts include currant and gooseberry shrubs in the genus Ribes. On infected five-needle pines, white pine blister rust causes formation of resinous cankers that commonly girdle host stems, especially those of 20cm or smaller diameters. Girdling results in branch and top mortality of large trees, and, in the case of



main stem infections on smaller hosts. frequently causes death of the entire tree. Large infected trees that are not killed immediately by the fungus may be predisposed

to infestation by mountain pine beetle. White pine blister rust also has the potential to reduce cone production by killing cone-bearing branches (McKinney and Tomback 2007). In the Pacific Northwest, reported levels of infection of living trees in surveyed stands where blister rust was present varied from 17 to 92 percent.

Mountain Pine Beetle

The mountain pine beetle (Dendroctonus ponderosae) is the primary agent of insect-caused mortality in both lodgepole pine and whitebark pine. During the historically warm years of the 1930s, mountain pine beetles killed many clusters of whitebark pines (Perkins and Swetnam 1996). Between 2005 and 2007 an estimated 600,000 whitebark pines

were killed by mountain pine beetles in Washington and Oregon.

Mountain pine beetles preferentially attack the largest trees first, and large trees produce more beetles per unit area of bark because of their greater circumference



and height (Cole and Amman 1980). Because weakened trees are more easily colonized than vigorous trees, it would be expected that white pine blister rust infection would make a whitebark pine more susceptible to attack. However, the evidence for such a relationship has not been firmly established (Kegley et al 2003). Nevertheless, the combination of mountain pine beetles killing larger trees and white pine blister rust killing smaller trees has been particularly destructive to whitebark pine populations.

Fire

Fire is a natural component of whitebark pine ecosystems. Low- and moderateintensity fires keep fuel loads low and reduce competition from later seral conifers, shrubs, and dense grasses. Highintensity fire provides newly opened areas in which whitebark pine can successfully germinate and grow without competition. Absence (exclusion) of fire due to active fire suppression has led to replacement of whitebark pine by more shade-tolerant, later seral conifer species and has reduced regeneration opportunities for whitebark pine (Keane et al. 2002, Kendall and Keane 2001). Additionally, whitebark pine may currently be at a point of lowered fire tolerance due to the impacts of blister rust and increasing levels of mountain pine beetle activity (Kurth, pers. comm., 2008). Large high-severity fires have the potential to severely reduce or even eliminate cone-bearing whitebark pine across an extensive landscape. If a fire becomes intense and widespread enough that most or all conebearing whitebark pines within the fire perimeter are killed, seed from unburned stands within nutcracker caching range may be available to regenerate whitebark pine in the burned area. If there is no such seed source, natural regeneration of whitebark pine will be extremely slow, or the species may become locally extirpated.



Robin Shoal, USFS



Global Climate Change

Whitebark pine may be particularly vulnerable to loss of favorable habitat due to the restriction of its range to the upper subalpine zone. The predicted impacts of warming temperatures include a severe decline in suitable habitat; increased mountain pine beetle activity; an increase in the number, intensity, and extent of wildfires; and perhaps an increase in white pine blister rust-related mortality. The present lack of scientific tools to predict climate change on regional or local scales limits the ability to quantify potential future impacts that can be applied to management decisions at the forest or stand level. However, a number of new

initiatives that focus on the impacts of climate change on western forests will provide information and tools that can be used to create management strategies for whitebark pine in the Pacific Northwest that incorporate climate change. Part of the regional 5-year action plan is the development of specific management recommendations for whitebark pine and associated species that incorporate the best available science on the predicted impacts of climate change on whitebark pine.

THE PACIFIC NORTHWEST REGION COMPREHENSIVE 5-YEAR RESTORATION PLAN

- Develop and implement a plan to plant priority management units.*
- Collect seed to meet gene conservation, rust resistance screening, and planting objectives.*
- Assess the condition and determine restoration needs for all priority management units.*
- Develop and implement a plan to plant priority management units.*
- Continue the ongoing rust screening program with emphasis on seed zones in grizzly bear recovery areas.
- Develop and implement a plan to treat mountain pine beetle in high risk units.
- Develop an approach for planting in designated wilderness areas that will allow the use of resistant plant material while maintaining wilderness character.
- Develop an approach to mitigate the predicted impacts of climate change.
- Develop monitoring plan(s) to track accomplishments, measure success of actions, provide information and feedback to improve procedures and outcomes of projects, and disseminate information.
- Work collaboratively to meet information needs.

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TOP TEN MANAGEMENT AND RESEARCH QUESTIONS

- 1. What is the influence of climate change on the life cycles of C. *ribicola*, seed and cone insects, and mountain pine beetle in the Pacific Northwest?
- 2. How are fuel management dynamics best managed in different parts of whitebark pine's habitat?
- 3. How often and where would prescribed fire benefit different parts of whitebark pine's habitat and what would be the effects on mountain pine beetle activity?
- 4. Do whitebark pine seedlings survive and grow better when they occur in a close group (as is often the case in nature when they are planted by nutcrackers) than when they occur as widely spaced individuals?
- 5. What are the influences of various kinds of micro-sites on success of whitebark pine planting?
- 6. What type of site preparation is necessary and best for successful planting of whitebark pines?
- 7. Is it possible to successfully direct-sow whitebark pine seeds in the field?
- 8. How can thinning of trees be incorporated with other techniques such as prescribed fire to maintain whitebark pine habitat and deter mountain pine beetle attack?
- 9. How would thinning affect mountain pine beetle activity in different stand and landscape conditions?
- 10. What information is needed to make meaningful dynamic models of whitebark pine habitat in a changing climate scenario, including models that could provide site-specific information to managers for determining the best places to undertake restoration efforts?

^{*}For details, see part 2 of this document.

PART 1: WHITEBARK PINE BIOLOGY, ECOLOGY, GENETICS, AND THREATS

INTRODUCTION

Goal

The goal of this restoration strategy is to summarize existing information regarding the biology, ecology, and genetics of whitebark pine (Pinus albicaulis Engelm.) in the Pacific Northwest; describe threats to the species; and identify a management approach for whitebark pine in the U.S. Forest Service's Pacific Northwest Region (Region 6). The future of whitebark pine is of substantial concern in Oregon and Washington as well as throughout its range because of the species' acute vulnerability to infection by the nonnative fungus Cronartium ribicola (which causes white pine blister rust), its high susceptibility to infestation by mountain pine beetle (*Dendroctonus ponderosae*), its risk of being destroyed in large and intense wildfires, and the likelihood of its being replaced in some subalpine mixed conifer forests by more shadetolerant tree species, a trend that is exacerbated by fire exclusion. There are also significant concerns about the impacts of climate change, particularly warming,

on this high-elevation, cold-adapted species. There is a recognized need to develop a proactive strategy that will provide the framework for promoting and maintaining healthy, reproductively successful whitebark pine stands in ecologically appropriate locations across the species' range in the Pacific Northwest. In the absence of timely management activities, there is reason to believe that the currently observed decline of whitebark pine will continue and may become irreversible, particularly in some locations.

This document represents the culmination of the Forest Service Pacific Northwest Region's 4-year whitebark pine program, which began in 2005. The long-term goal of the whitebark pine program is to sustain a network of viable populations of whitebark pine and associated species throughout the Pacific Northwest. The objectives of the regional effort were to (1) complete health status and genetic assessments, (2) accelerate seed sampling for blister rust resistance screening and gene conservation, and (3) develop a conservation and restoration plan.

How This Strategy is Organized

This strategy is divided into two parts. Part 1 provides background information on whitebark pine biology and ecology. The four threats to the species—white pine blister rust, fire, mountain pine beetle, and climate change—are discussed. The relationship between whitebark pine and the animals that disperse (and predate on) its seed is described in the section on Seed Fate. Because the whitebark pine genetic resource is critical for its conservation and for the development of blister rust resistant material, the genetics of the species is discussed in some detail. Part 2 includes the results of an ecoregion-based assessment and the development of a 5-year whitebark pine restoration program based on the assessment. The section on the Genetic Restoration Program summarizes the development of seed zones and seed transfer guidelines, gene conservation, the blister rust resistance testing program, and tree selection and seed collection. Opportunities for research and monitoring are given at the end of part 2.

The two parts and each section within each part can be read independently. Two appendices offer maps of whitebark pine habitat and tables of information that provide details of the results of the assessment.

Scope

This restoration strategy is intended to be applicable to the range of whitebark pine on National Forest System lands in Region 6 for the period 2009 through 2013. The information used in this strategy is the most current available, but additional useful research and monitoring results are likely to become available in the future. This strategy is intended to be reevaluated and refined as necessary in 5 years, using new information as appropriate. There may also be opportunities at that time to more closely coordinate this strategy with those of other regions and agencies. The strategy is intended to be used in conjunction with a companion Land Managers Guide (Shoal et al. 2008), which provides additional details on planting design and other specific restoration techniques in the Pacific Northwest.

Management Status

Whitebark pine is not currently a federally listed threatened or endangered species in the Pacific Northwest, although it is listed by the U.S. Fish and Wildlife Service as a species of concern in northwestern Washington and is currently under review for ranking by the Oregon and Washington Natural Heritage Programs.

A large percentage of the whitebark pine in the Pacific Northwest is on land administered by the Forest Service Region 6, which thereby exerts considerable influence on the fate of whitebark pine in the Pacific Northwest. Most whitebark pine occurs at high elevations in often inaccessible locations; the species has little or no commercial value as a timber species; and more than half the whitebark pine on National Forest System land occurs in congressionally designated wilderness areas where management interventions are constrained and commodity extraction is prohibited by policy. For these reasons, threats to whitebark pine are not directly tied to overexploitation or lack of protection of its physical habitat. Nonetheless, the threats to this species do have anthropogenic causes, including: non-native disease impacts, impacts of fire and fire exclusion, and effects of large-scale climate change, which may

include improved habitat for mountain pine beetles. Consequently, informed scientists and land managers have expressed increasing interest in developing a restoration strategy that addresses the threats to whitebark pine.

CLASSIFICATION AND DESCRIPTION

Systematics

Whitebark pine (*Pinus albicaulis*) was described by Engelmann in 1863. It belongs to the family Pinaceae, the genus *Pinus*, subgenus *Strobus*, and subsection *Cembrae*. It differs from all other North American pine species in its cone morphology and method of seed dissemination. Its closest relatives are the Eurasian stone pines *P.cembra*, *P. siberica*, *P. pumila*, and *P. koraiensis* (Lanner 1996).

Description

Whitebark pine is a medium-sized tree with characteristics adapted for survival in high mountains (Arno and Hoff 1990, Hitchcock and Cronquist 1976, Kral 1993). It commonly reaches heights of 7 to 20 m and may occasionally be as tall as 30 m on especially favorable sites. It has a straight to twisted trunk and a spreading conical, rounded, or irregular crown. Multiple stems representing a single tree or several very closely associated trees are common in open stands. At the high end of its elevation range on exposed sites where hurricane-force winds are common in winter, it assumes a stunted, krummholz form. Even in less inhospitable locations, whitebark pine frequently exhibits a picturesque, wind-swept appearance.

The species' thin bark is pale gray and appears whitish at a distance, hence its common name. Smooth on young trees, bark separates into plates with age. Whitebark pine branches are spreading or somewhat ascending and often persist on much of the trunk. Branchlets are tough and flexible. Needles are borne five per fascicle, are upturned and

connivent, are relatively short (3 to 7 cm long), and of a deep yellow-green to dark green color whitened on the adaxial side by stomates. Pollen cones are bright carmine. Seed cones are dark purple, very resinous, and range in length from 5 to 8 cm; they are short-stocked or sessile, usually occur in clusters

of two to five, remain on the tree unless dislodged by animals, and do not open except as a result of animal activity. Cones are generally ovoid with scales that are very thick distally and terminated by blunt tips; seeds are large (7 to 11 mm long), dark brown, and wingless.



Young whitebark pine showing light-colored stem and characteristic crown form and color.



Mature whitebark pine exhibiting multiple stems and rounded crown.



Pollen cones on a whitebark pine.



Whitebark pine seed cone.

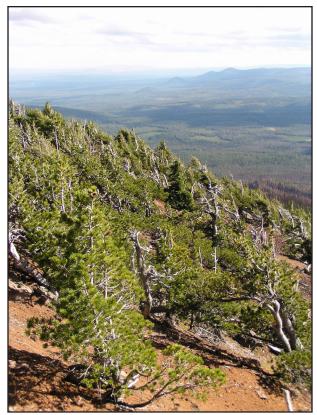


High-elevation whitebark pine habitat.

BIOLOGY AND ECOLOGY

Habitat

Whitebark pine grows at the highest elevations of any western tree species (Kral 1993, Arno and Hoff 1990). In Oregon and Washington, it occurs mainly at elevations of 1,600 m to 2,800 m. Annual precipitation varies from greater than 300 cm per year in the northern and western parts of its Pacific Northwest range to 50 cm per year in the southeastern portion. It is most successful on exposed ridges and drier sites and aspects (Ward et al. 2006b). Whitebark pine habitat is characterized by severe conditions (Arno and Hoff 1990), including: short, cool, often droughty summers; growing seasons of fewer than 110 days; and frosts and even snow showers during summer months. Winters are long and snowy, with severe windstorms in which wind speeds reach and exceed 100 km per hour. Winter low temperatures average -5° C and may be as low as -40° C. Whitebark pine grows on a variety of soil types, most of which are immature, poorly developed soils with high rock content (Arno and Hoff 1990).



s Jensen, USFS

Range, Distribution, and Abundance

Whitebark pine occurs in the mountainous regions of western North America (Kral 1993). Outside the Pacific Northwest states, it is distributed in the British Columbia Coast Range Mountains and Cascades, the Rocky Mountains from British Columbia and Alberta to Wyoming, the Sierra Nevada and Klamath Mountains of California, and in some of the high Great Basin ranges of Nevada (fig. 1). In Washington and Oregon, it grows in the Cascade Range and in the Olympic, Kettle River, Selkirk, Blue, Wallowa, Paulina, Yamsey, North Warner, and Siskiyou Mountains (Ward et al. 2006b).

Whitebark pine populations tend to be scattered and spotty because of the often discontinuous distribution of favorable habitat on high mountain peaks and ridges. Individual populations are of widely varying sizes, with some being quite small. Along the north—south running Cascades where the largest numbers of whitebark pine populations in the Pacific Northwest occur, the drier regions east of the Cascade Crest (the Eastern Cascades Section in Bailey's ecoregion classification system [Bailey et al. 1994]) commonly have more suitable habitat than areas farther west (Bailey's Western Cascades Ecoregion) (Ward et

Figure 1. Range of whitebark pine (USGS 1999)

al. 2006b). Some Pacific Northwest whitebark pine populations, notably those in the Olympic and Blue Mountains, are widely separated from any other populations, and the populations in northeastern Washington are closer to the Rocky Mountain portion of the species' range than they are to the Cascades. Figure 2 shows the currently known distribution of occupied and potential whitebark pine habitat in Oregon and Washington.

Most whitebark pine habitat in Washington and Oregon occurs on federally administered land, and 81 percent is on lands administered by the Forest Service, Region 6. Sixty percent of the known occupied whitebark pine habitat and 72 percent of the potential whitebark pine habitat on National Forest System land in the Pacific Northwest occurs in congressionally designated wilderness areas. Whitebark pine was detected in 334 (2.2 percent) of the 15,232 continuous vegetation survey (CVS) and Forest Inventory and Analysis (FIA) plots distributed systematically across Oregon and Washington that were evaluated from 1991 to 2000 (Goheen et al. 2002). For comparison's sake, among other five-needle pine species, western white pine was detected in 1,235 plots (8.1 percent) and sugar pine (Pinus lambertiana) was detected in

> 678 plots (4.4 percent). In terms of numbers of whitebark pine trees per unit area, one 21-transect survey involving 168 plots done in the southern Cascades showed a mean of 129 live trees of all sizes per ha, with a range for individual transects of from zero live whitebark pines per ha to 509 per ha (Goheen et al. 2002). Eightyseven percent of these trees were small (less than 5 m tall), and many of the small trees (49 percent) were infected by the white pine blister rust fungus. A 30-stand survey in the Blue Mountains (Erickson, unpublished data) showed a mean of 289 live whitebark pines of all sizes per ha with a range for individual stands of 20 to 739 live whitebark pines per ha. Seventy-eight percent of these trees were small (10 cm or less in diameter).

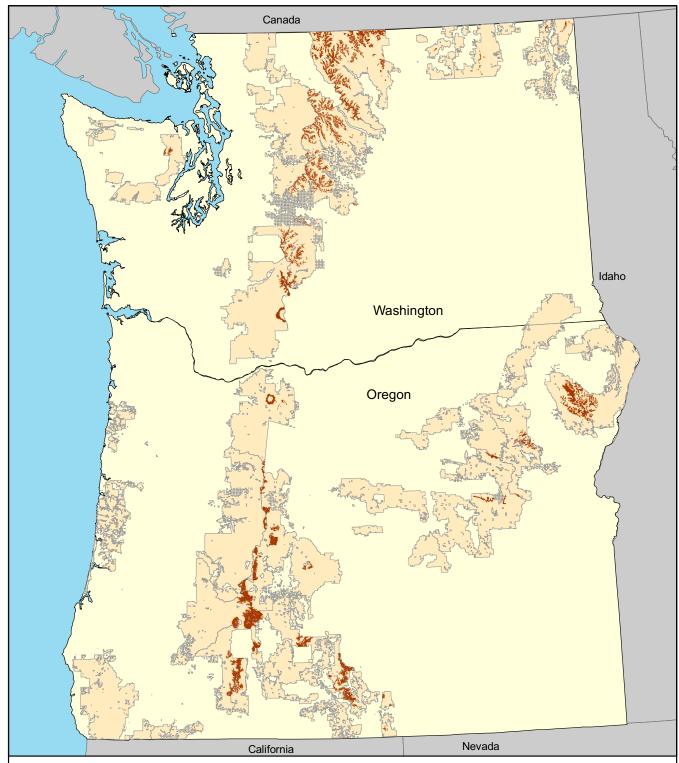


Figure 2. Whitebark Pine Habitat on National Forest System Lands U.S. Forest Service Region 6







Whitebark Pine Habitat



National Forest System Lands

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HOW WHITEBARK PINE HABITAT WAS MAPPED

We considered a number of possible surrogates for whitebark pine habitat and settled on plant association groups (PAGs). The PAGs are well-documented by the various Region 6 area ecology programs; they are familiar to and used regularly by Forest Service personnel. We used PAG spatial data in 30-m-resolution grid format for most of the region, with these exceptions: for the Gifford Pinchot National Forest we used potential natural vegetation (PNV); and for the Wallowa-Whitman National Forest we obtained an existing layer created for whitebark pine based on stand exams. We used a geographic information system (ArcMap version 9.1, ESRI 2005) to intersect these layers with a point dataset that represents documented whitebark pine locations across the region. This non-random dataset includes Forest Inventory Analysis (FIA) and continuous vegetation survey (CVS) plots, area ecology plots, a North Cascades grizzly bear habitat study, Pacific Northwest Albicaulis Project survey and reconnaissance data points, reconnaissance and survey points from other sources, all the whitebark pine cone collection sites in the region, and verified sites from other reliable sources. This dataset represents the full gamut of whitebark pine presence—from FIA plots in which only a single whitebark pine sapling was recorded, to upper subalpine sites where whitebark pine is the climax tree species.

In general, whitebark pine presence corresponds most closely with PAG 3201, parkland. In Washington, the correlation between parkland habitat and whitebark pine presence weakens near and west of the Cascade Crest; the climate becomes moister and milder, favoring other conifer species, and whitebark pine is limited to the highest, most inhospitable slopes and ridges. The parkland PAG over-represents whitebark pine habitat in both Mt. Rainier and North Cascades National Parks, on the Mt. Baker-Snoqualmie National Forest, and in the Olympics. Whitebark pine occurs only rarely on the Mt. Baker-Snoqualmie National Forest; most occurrences are near the Cascade Crest or in rainshadow areas like Crystal Mountain, northeast of Mt. Rainier. In the Olympic Mountains, whitebark pine is restricted to the rainshadow region in the northeast corner of the range.

The parkland PAGs represent the fundamental niche for whitebark pine "source" populations. Lower elevation habitat can and does support whitebark pine in the Pacific Northwest and is part of the species' overall fundamental niche, However, these lower elevation stands are typically mixed-species stands where whitebark pine is a minor or early seral component that rarely reaches reproductive capability; in that sense this is effectively "sink" habitat. Even within the habitat represented by the parkland PAGs, not all of the area is actually occupied by whitebark pine. The places where reproductive whitebark pines actually grow constitute the realized niche, or source habitat, for this species. It is these portions of the habitat that are the primary focus of this restoration strategy.

Life History

Life Cycle

Whitebark pine is monoecious, and trees begin to produce cones at about age 20 to 30 years (Krugman and Jenkinson 1974). Male cones are produced throughout the tree's crown on new-year's growth while female cones develop near the tips of upper crown branches. As with most pines, time from first inception of the female cone to maturation of the seeds is 2 years. Pollen is shed by male flowers and acquired by female strobili from late June to early July of the first year. Fertilization actually takes place 13 months after pollination, and the female cones then grow rapidly, ripening in September of the second year. Large cone crops (many cones on pines over an entire



Chris

First year and second year (mature) cones.

stand) are produced at irregular intervals. Individual mature whitebark pines produce cones at 3- to 5-year intervals (Krugman and Jenkinson 1974). At a stand level, there may be some cones produced in most years, but many crops are small. It is believed that large cone crops are produced at shorter intervals in the southern part of whitebark pine's range than in the northern portion (Arno and Hoff 1990).

Seed Dissemination

Seed dissemination by whitebark pine is unique among American pines. The species' large, wingless seeds are rarely if ever spread by wind or gravity. Although a few seeds may fall from cones directly onto favorable seed beds near a parent tree, the number is believed to be small (Arno and Hof 1990), and whitebark pine cones lack the coarse shrinkage fibers that spread cone scales in other pine species to release seeds (Lanner 1996). Instead whitebark pine seeds are mostly released from cones and disseminated by a bird species, the Clark's nutcracker (*Nucifraga columbiana*).

Numerous seeds buried in soil caches but not reclaimed by nutcrackers germinate, usually after two or more winters, and grow—resulting in successful whitebark pine regeneration. Whitebark pine seedlings are commonly found in small clumps, reflecting the fact that the seeds from which they grew were originally cached together by a nutcracker.

For an in depth discussion of whitebark pine seed dispersal, see Seed Fate section.

Seed Maturation and Germination

Whitebark pine seeds exhibit marked variability in component maturity at the time when seed coats become hard (Arno and Hoff 1990, Tillman-Sutela et al. 2007). In many cases, the embryos and megagametophytes are still immature, and storage reserves (especially starches) remain in unstable form. In nature, this is probably an adaptive advantage for maintaining viability and staggering maturity over

several years when seeds are planted in soil by nutcrackers. However, it can also result in poor germination success when seed is collected for growth in nurseries. Nursery germination rates for untreated first year whitebark pine seeds may be as low as 10 to 15 percent. Greatly improved results can be achieved through a controlled pre-treatment of seeds that mirrors the processes



Newly germinated whitebark pine clump arising from a nutcracker cache.



A group of Clark's nutcrackers harvesting whitebark pine seeds.

in natural soil seed banks. A 3- or 4-month multistep treatment that includes soaking, warm and cold stratification, and seed-coat abrasion by cutting or sanding can raise first year seed nursery germination success to 80 percent or more (Burr et al. 2001, Berdeen et al. 2006).

In nature, whitebark pine germination is epigeal, and newly germinated seedlings are large compared to seedlings of other high mountain conifers. Whitebark pine is a slow-growing tree that usually develops a deep, widespread root system and has the potential to attain great ages. Whitebark pines 700 to 1,000 years old have been reported (McCaughey and Schmidt 1989). The species has a remarkable ability to live with cold temperatures and high winds. Whitebark pine is capable of layering, most notably when in its krummholz form. It can also be grafted quite readily to rootstocks of other subgenus *Strobus* pine species such as western white pine (*Pinus monticola*) (Arno and Hoff 1990).



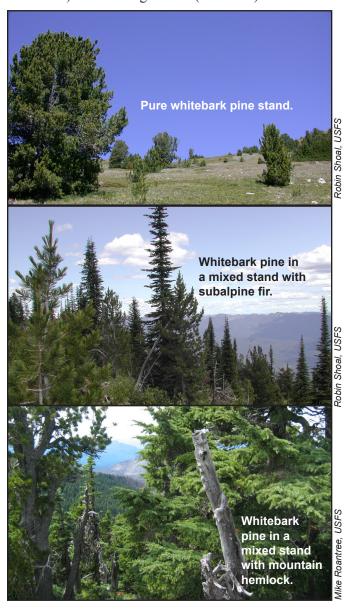
Clump of young whitebark pine seedlings.

in Shoal, USFS

Ecological Considerations

Competition

Whitebark pine is classed as intolerant to competition (McCaughey and Schmidt 1989). Common tree associates of whitebark pine in subalpine mixed conifer stands of the northern part of the Pacific Northwest include subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and lodgepole pine (*Pinus contorta*) (Ettl 2006). Farther south, these species may still be present, but mountain hemlock (*Tsuga mertensiana*) becomes increasingly important, western white pine is sometimes an associate, and, in southern Oregon, Shasta red fir (*A. magnifica* var. *shastensis*) becomes significant (Ettl 2006).



Whitebark pine is more shade-tolerant than lodgepole pine and about the same as western white pine (Arno and Hoff 1990); other associates are substantially more shade-tolerant than whitebark pine is. At the high end of its elevation range and on exposed or dry sites where conditions are too extreme for other tree species, whitebark pine may grow virtually alone and be the climax species. At lower elevations where more hospitable weather conditions prevail and whitebark pine is a component of subalpine mixed conifer forests, it is frequently the pioneer species that grows first on a site following disturbance and provides the cover that eventually allows more shade-tolerant tree species to become established. In the absence of additional disturbance, whitebark pine may be outcompeted and replaced over time in such subalpine mixed stands by the more shade-tolerant true firs, spruces, and hemlocks.

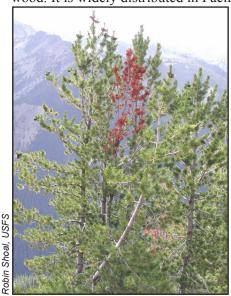
Undergrowth plant species commonly associated with whitebark pine in Washington and northern Oregon include grouse whortleberry (Vacinium scoparium), mountain arnica (Arnica latifolia), red mountain heath (Phylodoce empetriformis), rusty leaf menziesia (Menziesia ferruginea), smooth woodrush (Luzula hitchcockii), beargrass (Xerophyllum tenax), elk sedge (Carex geveri), Ross sedge (C. rossii), Parry rush (Juncus parryi), and Idaho fescue (Festuca idahoensis). In central and southern Oregon, common undergrowth associates include grouse whortleberry, beargrass, common prince's pine (Chimaphila umbellate), pinemat manzanita (Arctostaphylos nevadensis), long-stolon sedge (C. pensylvanica), and Wheeler bluegrass (*Poa nervosa*). Competition with undergrowth plants is believed to negatively affect whitebark pine seedlings and saplings, especially on moister sites where undergrowth is most dense (Arno and Hoff 1990). Alternatively, low-growing plants on severe sites may protect small whitebark pines after germination. Research on the interactions between whitebark pine and associated plant species in Oregon and Washington is lacking and badly needed, as is research on possible manipulation techniques for competing trees and undergrowth plants such as prescribed burning, mechanical thinning, and soil scarification.

Disturbance

Major physical disturbance processes that influence whitebark pine are landslides and fires. Locally, landslides can kill all or most of the trees in an area. The influence of fire on whitebark pine is complex and can be very different depending on fire intensity and size and the type and distribution of trees in an area. Whitebark pine is thin-barked and not very resistant to fire but may escape serious injury even in high-intensity fires in areas where it has a widely scattered distribution and fuel levels are low. As already mentioned, whitebark pin e has a significant role in pioneering the reforestation of areas disturbed by fires or landslides.

Pathogens

Native pathogens of whitebark pine cause few significant impacts (Hepting 1971). The species is affected by several foliage pathogens. Brown felt blight (caused by the fungi *Neopeckia coulteri* or *Herpotrichia juniperi*) is the most commonly observed, occurring on whitebark pine throughout the species' range in the Pacific Northwest. Infection can result in mortality of foliage and branches that are covered by snow in winter. Whitebark pine is also affected by several canker fungi, the most common of which is *Atropellis piniphila*. This pathogen induces branch cankers with associated dark staining in host wood. It is widely distributed in Pacific Northwest



Blister rust infection often kills branches resulting in red "branch flags".

whitebark pine stands and can cause some branch and tip dieback.

Whitebark pine is considered to be a secondary host of three species of dwarf mistletoe: lodgepole pine dwarf mistletoe (Arceuthobium americanum), limber pine



This blister rust canker on a small whitebark pine branch shows characteristic swelling and ruptured bark.

Robin Shoal USES

A blister rust canker on the bole of a whitebark pine. The orange margin is symptomatic of the disease.



Robin Shoal, USFS



White pine blister rust canker with aeciospores on the main stem of a whitebark pine.

Richards Sniezko, USFS

dwarf mistletoe (A. cyanocarpum), and mountain hemlock dwarf mistletoe (A. tsugae subsp. mertensianae). The first two have been reported on whitebark pine in central Oregon near Sisters, and the latter from the southern and central Oregon Cascades at Crater Lake and Mackenzie Pass and the eastside of the central Washington Cascades near Lake Chelan (Hawksworth and Wiens 1996). Dwarf mistletoes are parasitic flowering plants that rely on their hosts for nutrients and water. Heavy infections of any of these dwarf mistletoes can cause formation of "witch's brooms," top and branch mortality, and vigor decline in whitebark pine. Impacts are locally severe, but none of these dwarf mistletoes is distributed widely enough on whitebark pine to have consequential effects on any substantial portion of the species' population.

An introduced fungus, *Cronartium ribicola*, which causes white pine blister rust, is by far the most damaging pathogen that affects whitebark pine (Hepting 1971). It frequently kills small trees (those under 20 cm diameter at breast height) and causes branch and top mortality of larger trees. See the Threats to the Species section for more details.

Insects

Most insects that occur on whitebark pine are not very damaging (Furniss and Carolin 1977). Few insects are known to feed on whitebark pine foliage in the Pacific Northwest, and those that do (an aphid, Essigella gillettei, and a moth, Argyrotaenia tabulina) have not been reported to have noticeable impacts on the species. Whitebark pine is a host of two species of mealybugs (Puto cupressi and P. pricei). These sucking insects feed on fluids obtained from branches and the main stem. They have not caused significant impacts on whitebark pine although there are reports of damage to other conifer hosts in mixed stands with whitebark pine. Secondary bark beetles, including Pityogenes spp. and Pseudips mexicanus, infest wounded, stressed, or dying whitebark pines in Oregon and Washington; and Pityopthorus spp. attack twigs and small branches.

Seed and cone insects may affect whitebark pine seed crops. Preliminary evaluations (Kegley et al. 2001) suggest that fir coneworms (*Dioryctria abietvorella*) and western conifer seed bugs (*Leptoglossus occidentalis*) are of greatest concern throughout the West. Both of these species have been found affecting whitebark pines in Washington and Oregon. Other possibly damaging seed and cone insects include pine cone beetles (*Conopthorus ponderosae*), adelgids (*Pineus* spp.), and stem-boring *Dioryctria* spp. A scarab beetle (*Dichelonys fulgida*) feeds on whitebark pine pollen. Impacts of seed and cone insects on whitebark pines need further investigation. If severe, cone protection, especially on select seed trees, may be necessary.

By far the most important tree-killing insect on whitebark pine is the mountain pine beetle (*Dendroctonus ponderosae*). This beetle is capable of infesting and killing whitebark pines of any size above about 12 cm diameter



Adult female mountain pine beetle.

at breast height, and its impacts can be significant (Furniss and Carolin 1977). See the Threats to the Species section for more details.

Ecological Role

Whitebark pine has been widely described as a "keystone" species in high-elevation forests (Tomback et al. 2001, Schwandt 2006). This tree certainly is an important ecosystem component that influences the success of other organisms. It plays a vital role in first colonizing areas disturbed by fire or landslides, stabilizing the soil, moderating snow melt, and providing the cover that allows regeneration of other tree species. In southern Oregon, it is also the main species to colonize openings in subalpine mountain hemlock stands caused by the virulent root pathogen Phellinus weirii (Goheen et al. 2002), to which whitebark pines are resistant. Although among wildlife species only the Clark's nutcracker plays an important part in whitebark pine seed dissemination, many other wildlife species of high-elevation ecosystems depend to varying degrees on whitebark pine seeds as food resources (Lanner 1996). Other birds known to feed on whitebark pine seeds include jays, ravens, grosbeaks, chickadees, and nuthatches. Mammals include mice, chipmunks, squirrels, and bears. Two species of squirrel, the red squirrel (Tamiasciurus hudsonicus) and the Douglas squirrel (T. douglasii), in particular, harvest large numbers of whitebark pine cones in good seed years and store them in midden piles for winter food (Lanner 1996, Mattson et al. 2001). Black bears (Ursis americana) and grizzly bears (*U. arctos*) harvest whitebark pine cones themselves but more commonly raid squirrel middens to take advantage of the concentrated, high-quality food represented by the pine seeds in them. A plentiful supply of whitebark pine seeds in squirrel middens has been shown to contribute substantially to the success of bear populations and also to reduce the amount of conflict between humans and grizzly bears (Mattson et al. 1992; Mattson et al. 2001). In northeastern Washington, the grizzly bear is a threatened species, so its welfare as it relates to whitebark pine is of considerable management importance. See the Seed Fate section, later in this document, for more details on the relationship of vertebrate animals to whitebark pine seed fate.

Population Trends

Recent population trends for whitebark pine are cause for management concern (Tomback et al. 2001, Schwandt 2006). The vigor and reproductive success of this species have declined markedly through much of its range in recent decades, and mortality is currently very high in the Pacific Northwest (Ward et al. 2006b).

Table 1 summarizes mortality levels documented in surveys for whitebark pine condition in Washington and Oregon national forests from 1992 to 2004. The table shows that at a stand level, mortality ranged from 2 to 41 percent of the whitebark pine trees.

In addition to large numbers of dead trees, many surveyed stands also contain high numbers of living whitebark pines that exhibit infection by white pine blister rust (table 2).

Since many white pine blister rust infections on smaller whitebark pines (20 cm diameter at breast

Table 1. Mortality documented in stand assessments of whitebark pine (all size classes) on national forests in the Pacific Northwest Region

| in the Facilic Northwest Region | | | | | | |
|---------------------------------|----------------|-------------------|--|--|--|--|
| National forest | Year of survey | Location | Mean percent mortality per stand | | | |
| Olympic | 2002–2003 | 3 stands | 25 | | | |
| Mt. Baker- Snoqualmie | 2003 | 3 stands | 41 | | | |
| Okanogan | 1996 | Trinity Mt, WA | 2 | | | |
| Okanogan | 2003 | 8 stands | 16 | | | |
| Okanogan | 2004 | 2 stands | 33 | | | |
| Colville | 2004 | 4 stands | 24 | | | |
| Wenatchee | 1996 | 3 stands | 12 | | | |
| Wenatchee | 2002 | 1 stand | 40 | | | |
| Mt. Hood | 2003 | 10 stands | 40 | | | |
| Umatilla and Malheur | 2002–2003 | 30 stands | 24 | | | |
| Wallowa- Whitman, | 2003–2004 | | | | | |
| Eagle Caps Elkhorn | | 100 100 | 27 73 | | | |
| Deschutes | 2004 | 5 stands | 33 | | | |
| Umpqua | 1998 | 21 stands | 10 | | | |

Source: Erickson et al. 2007, Ward et al. 2006b.

height or smaller) are main-stem infections, a high proportion of these trees are very likely to die or suffer top mortality in the next few years. Larger infected trees may survive for some time with greatly reduced vigor; large trees with substantial amounts of blister rust generally are poor cone producers.

Unfortunately, information on long-term whitebark pine population trends in individual stands in the Pacific Northwest is lacking. Remeasured permanent forest inventory plots containing whitebark pine are few and flawed because only trees greater than 12.5 cm are recorded. Comprehensive surveys of whitebark pine stands done at different points in time are currently nonexistent. Virtually all stand data available that evaluate pines of all sizes are from single, one-time examinations. The contention that whitebark pine is seriously declining in the region is based on high observed amounts of recent and current mortality due to fire, white pine blister rust infection, and mountain pine beetle infestation; documentation of very high levels of white pine blister rust on still-

Table 2. Prevalence of blister rust infection documented in stand assessments conducted on national forests in the Pacific Northwest Region

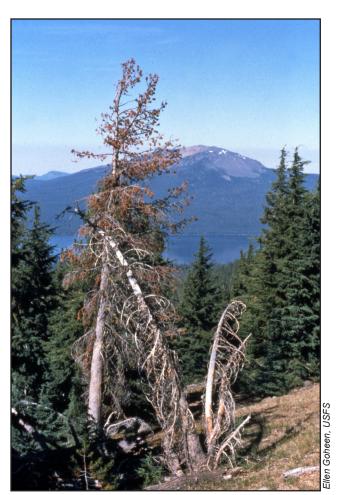
| National forest | Year of Survey | Location | Mean percent of living stems infected per stand |
|--------------------------|-------------------|-------------------|---|
| Olympic | 2002–2003 | 5 stands | 22 |
| Mt. Baker- Snoqualmie | 2003 | 3 stands | 76 |
| Okanogan | 1996 | Trinity Mt, WA | 27 |
| Okanogan | 2003 | 8 stands | 48 |
| Okanogan | 2004 | 2 stands | 52 |
| Colville | 2004 | 4 stands | 33 |
| Wenatchee | 1996 | 3 stands | 19 |
| Wenatchee | 2002 | 12 stands | 17 |
| Mt. Hood | 2003 | 10 stands | 51 |
| Umatilla and Malheur | 2002–2003 | 30 stands | 64 |
| Wallowa- Whitman, | 2003–2004 | | |
| Eagle Caps Elkhorn | | 100 100 | 24 8 |
| Deschutes | 2004 | 5 stands | 29 |
| Umpqua | 1998 | 21 stands | 46 |

Source: Erickson et al. 2007. Ward et al. 2006b.

living trees involving a large number of presumably lethal main stem infections; high proportions of trees with topkill caused by white pine blister rust that affects cone and seed production; and stand structures in which small white pine blister rust-affected trees represent by far the most numerous size class.

THREATS TO THE SPECIES

The major threats to whitebark pine in the Pacific Northwest are white pine blister rust, mountain pine beetle, fire (both too much and not enough in different situations), and large-scale climate change. All have been influenced or directly caused by human activities.



Decline and mortality of the whitebark pine component in a mixed stand.



Whitebark pine stand showing high levels of mortality from mountain pine beetle and white pine blister rust.

White Pine Blister Rust

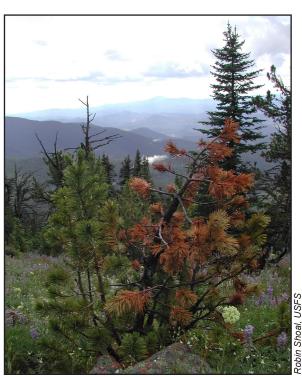
History

The pathogenic fungus Cronartium ribicola, which causes white pine blister rust, is native to eastern Asia. Starting in the late 1700s, the fungus spread across Europe in plantations of non-native pine hosts; in the early 1900s, it was introduced into both eastern and western North America on diseased pine planting stock from Europe (Boyce 1961, Hansen 2006). In western North America, introduction in 1910 resulted from a single consignment of infected eastern white pine seedlings shipped to Vancouver, British Columbia, from France (Benedict 1981). The pathogen became established in the wild near the site of introduction but was not recognized until 1921, by which time it had already spread into adjacent five-needle pine populations. Subsequent spread was remarkably rapid. By the early 1930s, white pine blister rust was common throughout southern British Columbia, Washington, northern Idaho, northwestern Montana, and northwestern Oregon, and in 1936 it was reported in southwestern Oregon and northwestern California (Mielke 1938, Benedict 1981).

Etiology and Life Cycle

White pine blister rust affects pine species in the subgenus *Strobus* (the five-needle pines). Alternate hosts of *C. ribicola* have long been known to include currant and gooseberry shrubs in the genus *Ribes*. Recently, it has been discovered that species of lousewort (*Pedicularis* spp.) and paintbrush (*Castilleja* spp.) also can serve as alternate hosts of the fungus (McDonald et al. 2006), although what roles they may play in the Pacific Northwest have yet to be determined.

On infected five-needle pines, white pine blister rust causes formation of resinous cankers that commonly girdle host stems, especially those of 20-cm or smaller diameters. Girdling results in branch and top mortality of large trees, and, in the case of main stem infections on smaller hosts, frequently causes death of the entire tree. Large infected trees that are not killed immediately by the fungus may be predisposed to infestation by mountain pine beetle. White pine blister rust also has the potential to reduce cone production by killing cone-bearing branches (McKinney and Tomback 2007). Heavy infection of the *Ribes* hosts may cause defoliation.



Mortality of a young whitebark pine caused by white pine blister rust.



Ribes sp.: one of the alternate hosts of the white pine blister rust fungus.

C. ribicola has a complex life cycle involving five spore types and requiring both pine and alternate hosts for its successful completion (Boyce 1961) (fig.3). Basidiospores of C. ribicola originating from alternate hosts infect five-needle pines during late summer and fall. Infection takes place through needles of any age. The relatively delicate, short-lived basidiospores are most commonly wind-dispersed, infecting pines within 100 m of the point of origin. For successful germination and infection to occur, there must be 48



Topkill of whitebark pine caused by white pine blister rust.

hours with 100 percent relative humidity and temperatures not exceeding 20° C during the time after spores have been deposited on host pine needles. Unfortunately, basidiospores in some cases can be carried in mist and fog that form in low areas, canyons, and valleys and move upslope as cloud banks. Such clouds provide moisture conditions favorable for spore survival; not infrequently, the clouds reach and stay at higher elevation areas where five-needle pine stands occur, contributing to pine infection at considerable distances from infected alternate hosts. This phenomenon is especially common in central and southern Oregon.



Fruiting bodies (telia and uredinia) of the white pine blister rust fungus on the underside of a *Ribes* leaf.

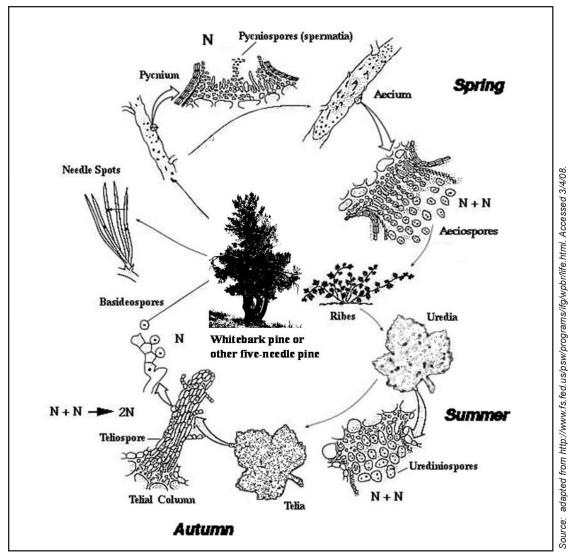


Figure 3. Life cycle of white pine blister rust.

Following C. ribicola basidiospore germination and successful penetration of a host pine needle, a sparse mycelium develops and grows from the needle into the bark of the pine stem. Twelve to 18 months later, a slightly swollen, cankered area first becomes visible. Two to 3 years after initial infection, pycnia and pycniospores are produced on the canker; the pycniospores are noninfective but they serve as gametes fertilizing other infections and leading to development of the highly infective aecia and aeciospores. Aecia form in the same location on the canker as the pycnia in the spring after an additional 12 to 24 months. The relatively tough aeciospores are wind disseminated over considerable distances (up to 500 km) and infect leaves of alternate hosts, particularly under moist conditions. Within weeks of infection, uredinia are produced on the leaves of alternate hosts. Urediniospores produced from the uredinia reinfect alternate hosts throughout the summer, causing buildup of inoculum. In late summer to early fall, hair-like telial columns emerge from the old uredinial pustules. Teliospores germinate in place on these columns and produce basidiospores, starting the process over again. The entire life cycle requires 3 to 6 years for completion (Boyce 1961).

Environmental Conditions

C. ribicola is clearly favored by moist, cool conditions at key times in its life cycle. Spread and infection are episodic and much more dramatic during years with moist summers and falls than in years when summers and falls are dry. Years with particularly favorable conditions and attendant high infection levels are known as wave years (McDonald and Hoff 2001). The disease is often not as severe on hosts growing in dry microsites as it is in moist ones, and hosts in entire areas with particularly dry summer and fall climates, such as southern Oregon east of the Cascades, are usually at much lower risk of disease than areas where conditions are wetter at that time of year. Even in such dry locations, though, hosts may suffer when infrequent wave years occur. Once C. ribicola is established in a pine host, it is perennial and relatively unaffected by weather conditions.

The magnitude of impacts caused by a non-native pathogen is often much greater than that associated with a native disease organism because hosts have not evolved with the introduced pathogen and thus have very little resistance to it. This is certainly the case with C. ribicola and five-needle pines in the western United States (Hansen 2006). Since its introduction, the pathogen has caused unprecedented amounts of decline and mortality of susceptible hosts in Oregon and Washington as well as other parts of the West. Although all the five-needle pine species that are native to the Pacific Northwest are susceptible to C. ribicola, whitebark pine was rated in early tests as the most highly susceptible (Spaulding 1929). Today white pine blister rust is distributed virtually throughout the Pacific Northwest range of whitebark pine except for a few dry areas in southeastern Oregon. The combined effects of white pine blister rust killing small trees and mountain pine beetles infesting mature trees is particularly destructive.

White pine blister rust clearly represents a very significant threat to the vitality and survival of whitebark pine in Washington and Oregon, as it does to the species in much of its range. Infection levels of C. ribicola and damage caused by the pathogen in whitebark pine stands are high in almost all areas where they have been evaluated, and are extremely high in many (Ward et al. 2006b). Mortality measured in most surveys (table 1, earlier) was not separated by cause, but white pine blister rust was believed to be the major contributor. In one survey where identification of cause of death was attempted, 84 percent of the mortality was attributed to white pine blister rust infection (Goheen et al. 2002). Reported levels of infection of living trees in surveyed stands where blister rust was present (table 2, earlier) varied from 17 to 92 percent. These are high levels when viewed from the perspective of the probability of additional mortality in subsequent years. Although past predictions were that levels of infection should be highest in the wetter, cooler portions of whitebark pine's range in the Cascades of northern Washington and be lower farther to the south where conditions are drier, survey results show high infection levels in the southern as well as the northern Cascades (Ward et al. 2006b).

Control

Efforts to control white pine blister rust initially were concentrated in areas where the economically valuable western white pine and sugar pine occurred; these efforts involved trying to break the disease cycle by removing the alternate hosts. Intensive and costly efforts aimed at eradicating *Ribes* were well-intentioned but singularly unsuccessful in practice in the Pacific Northwest (Benedict 1981, McDonald and Hoff 2001), as were attempts to kill the fungus in cankers with chemicals (Benedict 1981).

It has become increasingly evident that the most effective approach to controlling white pine blister rust involves promoting pines with various levels of resistance to C. ribicola (McDonald and Hoff 2001, Schwandt 2006, Schoettle and Sniezko 2007). Programs to identify and screen apparently resistant western white and sugar pines and to breed these species for increased resistance are well-underway and show great promise; however, C. ribicola's ability to mutate (and possibly to hybridize) means that precautions are necessary to maintain as many kinds of resistance mechanisms as possible in the breeding programs (McDonald and Hoff 2001, Hansen 2006). Whitebark pines with apparent resistance to C. ribicola have been identified in the field, and inoculation trials confirm that useful levels of resistance do exist (Schwandt 2006, Schoettle and Sniezko 2007).



Whitebark pine seedlings in a blister rust resistance trial.



Collecting cones from a whitebark pine that exhibits phenotypic resistance to white pine blister rust.

Mountain Pine Beetle

The mountain pine beetle (Dendroctonus ponderosae) is the primary agent of insect-caused mortality in both lodgepole pine and whitebark pine. The adult is a stout, black, cylindrical beetle about 6 mm long with clubbed antennae and powerful, chewing mouthparts. It ranges from the Canadian provinces of Alberta and British Columbia, through the western United States to northern Mexico. This beetle can infest and kill all species of native pines. It is most closely associated with the ecology of lodgepole pine and also has been known to cause significant mortality in whitebark pine (Logan and Powell 2001). During the historically warm years of the 1930s, mountain pine beetles killed many clusters of whitebark pines (Perkins and Swetnam 1996). More recently, between 2005 and 2007 an estimated 600,000 whitebark pines were killed by mountain pine beetles in Washington and Oregon.

Mountain pine beetle adults typically emerge from beneath the bark between late June and early September. A female initiates an attack on a host tree and produces an aggregation pheromone that attracts



Large, mature whitebark pines recently killed by mountain pine beetle.

both male and female beetles. The tree responds by producing pitch that can physically exclude attacking beetles, and resin that can impregnate egg galleries. If few beetles attack and the tree is fairly vigorous, these defensive mechanisms may prevent the tree from being killed. But even a very vigorous tree can be overcome if beetles attack in sufficient numbers. Adults mate, and females lay eggs along either side of their feeding gallery. Both larvae and adults feed upon the phloem just beneath the bark of the host tree. The tree is killed by the physical action of beetle feeding, and by two species of blue stain fungi that the beetles introduce when they penetrate the bark.

Mountain pine beetles usually have a 1-year life cycle, though 2 years may be required in cold climates at high elevations. Insect activity is highly correlated with temperature. Cold winter temperatures are a major source of mountain pine beetle mortality. During years of relatively mild winters and long summers, beetles will have increased winter survival and may be able to complete their life cycle more quickly.

Mountain pine beetles preferentially attack the largest trees first. Large trees produce more beetles per unit area of bark because of their greater circumference and height (Cole and Amman 1980). Because weakened trees are more easily colonized than vigorous trees, it would be expected that white pine blister rust infection

would make a whitebark pine more susceptible to attack. However, the evidence for such a relationship has not been firmly established (Kegley et al 2003). Nevertheless, the combination of mountain pine beetles killing larger trees and white pine blister rust killing smaller trees has been particularly destructive to whitebark pine populations.

When a tree is fully colonized by beetles, antiaggregation pheromones are produced to prevent overcrowding. These pheromones cause arriving beetles to fly by without stopping. Verbenone (4,5,5trimethylbicyclo [3.1.1] hept-3-en-2-one) is a known anti-aggregation pheromone that has shown promise in reducing mountain pine beetle attacks on susceptible trees (Kegley et al. 2003, Kegley and Gibson 2004, Gillette et al. 2006). Stapling two 5-gram pouches of verbenone to individual trees in mid June and replacing those pouches in late July has been shown to provide individual tree protection (Kegley et al. 2003, Kegley and Gibson 2004). In continuous stands of whitebark pine it may be possible to provide area protection by securing verbenone pouches to any available surface in a grid pattern at a rate of 30-40 pouches per acre. Tests are currently underway using a 7-g verbenone pouch that may release verbenone during the entire flight period, eliminating the need to replace pouches in mid season. Tests are also



Mountain pine beetle galleries under the bark of an infested whitebark pine.

en Goheen, USFS

underway using a verbenone flake that can be aerially applied. If these tests yield positive results, flakes could provide protection for whitebark pines in areas that are remote and difficult to access.

Individual tree protection also can be achieved by the application of carbaryl, a carbamate insecticide. The chemical is applied by spraying a liquid formulation sufficient to wet the entire bole of the tree from top to bottom prior to beetle flight. Attacking beetles will be killed on contact.

When any direct control of mountain pine beetle is planned, it is important to recognize that control efforts do not change the underlying environmental conditions that cause populations of this native insect to increase to damaging levels. However, direct control can be an important tool in maintaining trees and stands for cone collection or for recreation or aesthetic values.

There has been little study of landscape approaches for reducing mountain pine beetle damage in whitebark pine stands. However, whitebark pines growing in dense stands do respond to release with increased diameter growth (Keane et al. 2007), indicating improved tree vigor. Increasing vigor improves the likelihood that a tree will be able to successfully resist bark beetle attack, and may also increase cone production.



Mortality in whitebark pine caused by mountain pine beetles in a mixed species stand.

Fire

Fire is a natural component of whitebark pine ecosystems. Low- and moderate-intensity fires reduce competition from later seral conifers, shrubs, and dense grasses; such fires keep fuel loads low. High-intensity fire provides newly opened areas in which whitebark pine can successfully germinate and grow without competition. Whitebark pine is shadeintolerant (Arno and Hoff 1990) and is considered firedependent in fire-prone portions of its range (Tomback et al. 2001). This is particularly true in the Rocky Mountains, where extensive stands of whitebark pine forests occur in montane habitat and where the primary source of disturbance is fire. Whitebark pine, with its nutcracker-mediated ability to disperse seeds over much greater distances than its wind-dispersed competitors, becomes the pioneering tree species on recently burned areas (Bruederle et al. 2001). Absence (exclusion) of fire due to active fire suppression has led to replacement of whitebark pine by more shadetolerant, later seral conifer species and has reduced regeneration opportunities for whitebark pine (Keane et al. 2002, Kendall and Keane 2001). Returning and maintaining natural fire regimes is an important management action that can be taken to conserve whitebark pine in naturally fire-prone areas (Keane and Arno 2001).

In the Pacific Coast portion of its range, where the distribution of whitebark pine is both less extensive and more closely associated with upper subalpine and parkland habitat, the exclusion of fire from whitebark habitat is of lesser concern (Keane, pers comm., 2008). East of the Cascade Crest, natural ignitions in whitebark pine habitat are fairly frequent; however, because most of this territory is either in designated wilderness or otherwise remote, there is very little wildland-urban interface involved and therefore little cause for active fire suppression. The open character of the subalpine habitat provides ample territory for successful whitebark pine regeneration, provided there is a healthy seed source within nutcracker caching range. Fire is uncommon in the wetter regions near and west of the Cascade Crest, and whitebark pine

is typically restricted to windswept slopes and rocky ridges inhospitable to other conifer species.

Reported fire return intervals in subalpine forests east of the Cascades range from 29 years to 250 years (Agee 1993). Siderius and Murray (2005) found highly variable fire return intervals in 55 whitebark pine stands: 10 to 196 years in the Washington Cascades, with generally shorter intervals farther east of the Crest; and 39 to 142 years in the Oregon Cascades. Fire intensity also varied, with high-severity, standreplacing fires occurring about every 100 to 200 years, and low-severity fires occurring at intervals of as short as 9 years up to about 70 years.

When an ignition occurs in upper subalpine whitebark pine habitat, where stands are typically patchy and understory fuels are discontinuous, the fire is likely to remain both localized and of low to moderate severity. Whitebark pine is somewhat more resistant to fire than its later seral competitors (Agee 1993), so low-to-moderate severity fire is likely to benefit whitebark pine by reducing competing vegetation and keeping

fuel loads low. If cone-bearing whitebark pine trees within the stand are damaged or killed, seed from other trees within the stand or in nearby stands would ideally be available to support whitebark pine regeneration on the burned site.

Although fire can be beneficial for whitebark pine, too much fire can be detrimental. General climate warming is believed to be driving the current trend toward longer and more intense fire seasons in the western United States (Westerling et al. 2006). Ironically, in terms of long-term species survival, whitebark pine



Whitebark pine stand burned in the 1994 Tyee fire, Wenatchee National Forest.



Whitebark pine stand burned in the 2006 Tripod fire, Okanogan National Forest.

may currently be at a point of lowered fire tolerance due to the impacts of blister rust and increasing levels of mountain pine beetle activity (Kurth, pers. comm., 2008). Large high-severity fires—such as the 2006 Tripod Complex Fire on the Okanogan National Forest in Washington's northeast Cascades and the 2003 B & B Complex Fire on the Deschutes National Forest in the Oregon Cascades—have the potential to severely reduce or even eliminate cone-bearing whitebark pine across an extensive landscape. Subalpine fir is highly flammable, and a fire that moves into the crowns of this species is likely to be stand-replacing, especially where subalpine fir is relatively dense or within mature subalpine fir "islands" (Uchytil 1991). If they become plume-dominated, these crown fires are capable of sending sparks and cinders over distances in excess of a mile; resulting spot fires may enable the main fire to spread from the site of the original ignition (Bentley, pers. comm., 2008). If the fire becomes intense and widespread enough that most or all cone-bearing whitebark pines within the fire perimeter are killed, seed from unburned stands within nutcracker caching range may be available to regenerate whitebark pine in the burned area. If there is no such seed source, natural regeneration of whitebark pine will be extremely slow, or the species may become locally extirpated.

Global Climate Change

The Intergovernmental Panel on Climate Change (IPCC) projects that global average surface temperatures will rise about 1.8 to 4.0° C during the 21st century (IPCC 2007). The IPCC also recently concluded that "warming of the climate system is unequivocal" and "most of the observed increase in globally average temperatures since the mid-20th century is *very likely* due to the observed increase in anthropogenic (human caused) greenhouse gas concentrations" (IPCC 2007).

Whitebark pine may be particularly vulnerable to loss of favorable habitat due to the restriction of its range to the upper subalpine zone. The results of the application of one climate model indicate that suitable

habitat for whitebark pine will decline considerably by the year 2030 (Richardson et al., in press). Other predicted impacts of warming temperatures include increased mountain pine beetle activity; an increase in the number, intensity, and extent of wildfires; and perhaps an increase in whitebark pine blister rust-related mortality.

The present lack of scientific tools to predict climate change on regional or local scales limits the ability to quantify potential future impacts that can be applied to management decisions at the forest or stand level. However, a number of new initiatives focusing on the impacts of climate change on western forests will provide information and tools that can be used to create management strategies for whitebark pine in the Pacific Northwest that incorporate climate change. A few examples include:

- The Task Force on Adapting Forests to Climate Change (Howe et al. 2007);
- Forest management and climate change: a synthesis of genetic and silvicultural options for the Pacific Northwest (Howe et al. 2007);
- Decision support tools for determining appropriate provenances for future climates (Solomon 2008);
- A climate-driven forest vegetation simulator (Solomon 2008);
- A climate-change toolkit for western Forest Service managers and decision makers, incorporating climate change into everyday resource management (Solomon 2008);
- Tools to assess and assist vulnerable species at risk from climate change (Solomon 2008).

Part of the regional 5-year action plan (see part 2 of this document) is the development of specific management recommendations for whitebark pine and associated species that incorporate the best available science on the predicted impacts of climate change on whitebark pine.

SEED FATE

Summary

An understanding of how animals affect whitebark pine seed fate is important for the conservation and restoration of whitebark pine populations. Lorenz et al. (2008) provide a review of the literature on the mechanisms of whitebark pine seed fate. This section draws upon that literature review and other sources as noted.

Seeds are the primary means by which many species of plants, including whitebark pine, move across landscapes, colonize new areas, and ultimately maintain populations (Schupp and Fuentes 1995, Wang and Smith 2002, Vander Wall et al. 2005). Seed fate in whitebark pine is heavily influenced by biotic agents, particularly vertebrate animals, because whitebark pine seeds are large and valued as food by more than 20 kinds of seed-eating animals (Hutchins 1990). Seed fate pathways may end either in seed dispersal or predation (Vander Wall et al. 2005).

Four animals most commonly affect whitebark pine seed fate: Clark's nutcrackers, pine squirrels (*Tamiasciurus* spp.), chipmunks (*Tamias* spp.), and deer mice (*Peromyscus* spp.). These animals are specialized granivores and their life history traits revolve around conifer seed availability. Conifer seeds are produced only in autumn, and all these animals have therefore evolved strategies for storing seeds so that seeds can be consumed year round. Many seeds stored by these animals are never retrieved, and those seeds buried in favorable sites have the opportunity to germinate. While these animals act primarily as seed predators for whitebark pine, all of them also have the potential to act as seed dispersers.

The likelihood of a whitebark pine seed being dispersed to a favorable site varies depending on which species of animal stores the seed. Nutcrackers are generally considered the most effective seed disperser for whitebark pine because many of the seeds that nutcrackers store are placed in locations where



Clark's nutcracker harvesting seeds from whitebark pine cone.

the seeds can germinate and mature (Tomback 1978, Dimmick 1993). Pine squirrels are the least effective seed dispersers because few or none of the seeds that they harvest from trees are able to germinate into adults (Hutchins and Lanner 1982). The effectiveness of all these animals as seed dispersers can vary among years and locations, owing to many factors: variation between years in whitebark pine seed production, the availability of alternate foods for animals on a landscape scale, the suitability of whitebark pine stands as habitat for animals, and the size of animal populations. Overall, whitebark pine seed fate pathways are multifaceted, and whitebark pine seed dispersal is a dynamic process.

Seed Dispersal

Seed dispersal in plants has traditionally been considered a single-phase event in which an agent—such as animals, wind, or water—transports seeds from the parent tree to a suitable site of deposition where the seed can successfully germinate. More recent work has revealed that seed fate pathways for most plants are very complex. The first phase of seed dispersal, the transport of seeds from parent plants to the site of initial deposition, is usually followed by one to three secondary phases of seed dispersal.

Primary seed dispersal in whitebark pine has received a lot of study because most whitebark pine seeds are harvested from the parent tree by a relatively large and charismatic songbird called Clark's nutcracker. Nutcrackers are part of a guild of animals called scatter-hoarders; they store food during periods of food abundance in small stores that are scattered over the larger landscape. Nutcrackers forage on whitebark pine seeds when they are ripe and available each autumn. Seeds that are not immediately consumed by nutcrackers are scatter-hoarded, and nutcrackers forage on their seed stores for up to a year after storage. Many seeds are buried in the soil and in sites suitable for seed germination and seedling establishment. Some of these buried seed stores are never retrieved by nutcrackers over the course of a year, and these seeds are able to germinate.

Clark's nutcrackers act as primary seed dispersers for many species of conifer in North America in addition to whitebark pine. However, whitebark pine is unique among these pines because the seeds are produced in indehiscent cones. Nutcrackers use a long, woodpecker-like bill to chisel into the ripe but closed cones. Whitebark pine is unique because it is an obligate mutualist of Clark's nutcracker and it is believed that the regeneration of whitebark pine on a population-wide scale is dependent on these birds.

Secondary seed dispersal of whitebark pine seed has received little study, even though secondary seed dispersal of pine seed by chipmunks and deer mice occurs in other ecosystems where nutcrackers act as primary seed dispersers. In whitebark pine ecosystems, multiple field experiments have found that these rodents readily harvest seeds from whitebark pine cones, gather surface-sown seeds, and steal seeds from simulated nutcracker caches (Tomback 1982, Hutchins and Lanner 1982, Baud 1993). In one study, Tomback (1982) found that an astounding 82 percent of simulated nutcracker caches were pilfered by these thieving rodents. It has been assumed that all whitebark pine seeds gathered by chipmunks and mice are consumed.

However, relatively new research in *other* pine ecosystems has revealed that these rodents do not consume most of the seeds that they obtain. Rather, they scatter-hoard most seeds in new locations (Vander Wall and Joyner 1998). Chipmunks and deer mice are similar to Clark's nutcracker in their seedstoring habits; their caches of singleleaf pinyon pine (P. monophylla), Jeffrey pine (P. jeffreyi), and sugar pine (P. lambertinana) contained on average one to four seeds, which were buried 5 to 15 mm deep (Vander Wall 1992b, 1993, 1997; Thayer and Vander Wall 2005). As much as 69 percent of caches made by scatter-hoarding rodents survived to germination (Vander Wall 1995, Vander Wall and Joyner 1998). Therefore, it is not unlikely that chipmunks and mice do contribute to seed dispersal in whitebark pine, although this possibility needs to be verified.

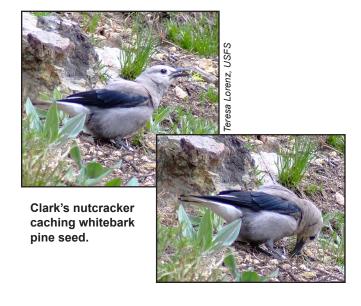


Robin Shoal, USFS

Seed Predation

Major invertebrate predispersal seed predators include cone worms and cone beetles (Bartos and Gibson 1990). Predispersal predators of whitebark pine seed also include the avian and mammalian granivores that forage on cones and collect fallen seed from the ground. Post-dispersal predators include granivores such as Clark's nutcracker, chipmunks, and the pine squirrel, and less specialized omnivores such as bears that consume seeds opportunistically.

Pine squirrels—red and Douglas squirrels (Tamiascuirus hudsonicus and T. douglasii)—are the most effective predispersal seed predators of whitebark pine because of their methods of seed harvest (Hutchins and Lanner 1982). Pine squirrels are part of a guild of animals called larder-hoarders because they store most of their seeds in one, centralized larder within their territory. It is common for cones and seeds to be buried within middens, which are piles of loose cone scales that have accumulated beneath favored feeding perches (Finley 1969, Vahle and Patton 1983). Seeds stored by pine squirrels are unlikely to establish as seedlings. Seeds are usually not extracted from cones before being stored, which precludes germination. Squirrels larder-hoard whitebark pine seeds in caches ranging from 14 to 55 seeds (Hutchins and Lanner 1982). Moreover, as squirrels cache and retrieve cones from their larders, materials are continually turned over, making establishment impossible for most seeds (Gurnell 1984, Hatt 1943).





Red squirrel.

Rodents and nutcrackers are also effective seed predators of whitebark pine in spring and summer because they forage on newly emerging whitebark pine germinants. Rodents forage on emerging seedlings opportunistically (Hutchins and Lanner 1982). Large flocks of nutcrackers seek out communal caching grounds in spring, where they systematically search for and consume they newly emerging whitebark pine seedlings (Vander Wall and Hutchins 1983, Lorenz and Sullivan, in prep.).

Seed Harvest and Caching Behaviors of Clark's Nutcracker

Nutcrackers forage on and harvest whitebark pine seeds and cones from mid summer through mid autumn (Tomback 1978, Hutchins and Lanner 1982, Dimmick 1993). Nutcrackers begin harvesting and caching whitebark pine seeds in the first week of August, and the peak of seed harvest is typically restricted to a 6-week period from mid August through late September (Tomback 1978; Hutchins and Lanner 1982; Dimmick 1993; Lorenz and Sullivan, in prep.). In years of low seed production by whitebark pine, essentially all seeds will be consumed by nutcrackers before the seeds have had an opportunity to mature, and few seeds are cached (Dimmick 1993). Conversely, in years of moderate or high cone productivity, each individual nutcracker caches an estimated 32,000 to 98,000 whitebark pine seeds (Hutchins and Lanner 1982, Tomback 1982, Dimmick 1993), or collectively about 95 percent of the available seeds (Dimmick 1993).

They recover seed stores primarily from winter through early summer (Tomback 1978; Vander Wall and Hutchins 1983; Lorenz and Sullivan, in prep.), so the site selected for seed storage is likely influenced by the accessibility of the site when snow is present. Nutcrackers commonly cache seeds in the soil (Vander Wall and Balda 1977; Tomback 1978; Hutchins and Lanner 1982). Seeds are buried 1 to 5 cm deep, and caches are made either by side-swiping the bill to create a slight depression or by directly probing into the ground with the bill (Tomback 1998). Slopes and cliffs used for placing below-ground caches often have southerly aspects and/or are very steep, and nutcrackers may select such slopes because of relatively rapid snow melt or low accumulation. In some instances, an entire population of nutcrackers may use one such slope for caching; these areas are called communal caching grounds.

Nutcrackers also commonly cache seeds above ground in the branches, bole, and bark of trees (Tomback 1978, Dimmick 1993, Lorenz 2007). Nutcrackers inhabiting different regions may have different preferences for below- or above-ground cache sites. In regions with lighter winter snow packs, for example, nutcrackers appear to place a higher proportion of caches below ground, whereas in regions with heavier snow packs nutcrackers may store most of their seeds in trees, where they will be above likely winter snow packs (Dimmick 1993, Lorenz 2007). Overall, it appears that individual nutcrackers respond to unique microclimatic conditions in their locality, and they choose above- or below-ground sites for seed storage accordingly.

There is a lot of variation in the distances nutcrackers transport seeds between harvest trees and cache sites (Vander Wall and Balda 1977, Tomback 1982, Dimmick 1993). Some individuals cache seeds a few meters from harvest trees, and others may transport whitebark pine seeds as far as 29.3 km (Tomback 1978, Dimmick 1993, Lorenz and Sullivan, in prep.). The distance that a nutcracker transports seeds is influenced by the migratory status of an individual and the location of an individual's home range. Non-

migratory, resident nutcrackers transport nearly all of their seeds to their year-round home range for storage. Lorenz and Sullivan (in prep) found that resident nutcrackers transported whitebark pine seeds on average 9.8 km between harvest trees and cache sites. In this same study, emigrant nutcrackers were observed transporting seeds much shorter distances, and all seed caches were placed within 2 km of the harvest trees. These differences in seed transport distance were partially explained by differences in seed retrieval behaviors in winter, spring, and summer; resident nutcrackers retrieved all caches from within their home range, whereas emigrants retrieved caches from communal caching grounds as they migrated through a region (Lorenz and Sullivan, in prep.). Regardless of the migratory status of an individual nutcracker, no other species of animal are known to transport whitebark seeds father than several meters from harvest trees and because of this, nutcrackers have the potential to contribute to genetic diversity in whitebark pine more so any other seed dispersal mechanism.

Impact of Declining Whitebark Pine on Clark's Nutcracker Populations and Seed Dispersal Effectiveness

Whitebark pine is declining throughout its range and there are concerns that nutcrackers are declining in numbers as well. This has raised valid concerns among land managers about the likelihood of three major outcomes:

- Throughout the range of whitebark pine, nutcrackers may become increasingly rare or even extinct before the effects of restoration are realized.
- In relatively isolated populations of whitebark pine, nutcrackers may become rare or locally extinct in the near future.
- In locations where whitebark pine has been absent for several generations, nutcrackers may never return or populations may not sufficiently rebound even if whitebark pine is successfully restored.



Clark's nutcracker with sublingual pouch filled with whitebark pine seeds.

In this section we review factors affecting the likelihood of each of these possible outcomes. Where appropriate, we suggest methods by which the effects of these outcomes might be mitigated.

Nutcrackers will likely persist within the range of whitebark pine even if restoration efforts are not fully realized for many decades because nutcrackers forage opportunistically on a wide variety of foods. Even where the range of whitebark pine and Clark's nutcracker overlap, whitebark pine seed is not necessarily the predominant food source for nutcrackers. Nutcrackers forage on insects, small mammals, and birds; they also forage on and store seeds of more than 10 species of conifers and one species of oak. Thus, while Clark's nutcracker has coevolved with whitebark pine, it is well-adapted to forage on other foods. For nutcrackers inhabiting forests in Region 6 that are east of the Cascade Crest, ponderosa pine and Douglas-fir are important alternative seed sources for Clark's nutcracker. Little is known about alternative seed sources for nutcrackers inhabiting forests west of the Cascade Crest. Presumably Douglas-fir and possibly pacific silver fir serve as alternative seed sources.

Small and isolated stands and heavily diseased stands of whitebark pine appear to be at the greatest risk of being abandoned and altogether ignored by seed-dispersing nutcrackers. On study sites in Arizona, Christensen and Whitham (1991) observed that nutcrackers were highly efficient in their harvest of seeds from pinyon pine trees. Trees with cones that

were diseased were ignored by flocks of seed-caching nutcrackers. Even more disconcerting, stands of trees with high infection rates were largely bypassed by seed-harvesting birds, even if these stands contained some uninfected trees. This study suggests that highly diseased whitebark pine stands may have few or no seeds dispersed, even if healthy cone-bearing trees are present. It also suggests that nutcrackers are likely to abandon isolated whitebark pine stands if cone production is especially low.

The composition of forests surrounding isolated whitebark pine stands in the Pacific Northwest may help to mitigate some of the effects of their isolation and diseased status. This is because nutcrackers respond to seed production by many species of largeseeded conifers and on a landscape scale. Many high-elevation whitebark pine stands in the Pacific Northwest are surrounded by a landscape that includes expansive stands of lower elevation ponderosa pine and Douglas-fir. Mixed stands of ponderosa pine and Douglas-fir provide suitable year-round habitat for nutcrackers. Nutcrackers in these areas may incidentally disperse seeds in isolated and diseased whitebark pine stands if they are attracted to the general region because of the presence of cone-bearing alternative seed sources. Conversely, whitebark pine stands within the Pacific Northwest that are isolated and surrounded by a landscape of less suitable forest types are likely to be at greater risk of being abandoned by nutcrackers. Relatively wet forests of hemlock (*Tsuga* spp.), fir, and spruce are poor habitat for nutcrackers because the seeds of these conifers are small and do not serve as alternative food sources. Isolated and diseased whitebark pine stands near or west of the Cascade Crest are likely at greatest risk of being abandoned by nutcrackers. Thus, nutcracker populations will benefit from effective management of both whitebark pine stands and lower elevation conifer forests.

Nutcrackers have evolved a nomadic life history strategy, and they readily migrate from areas where autumn cone productivity is low. Between years, these emigrating nutcrackers do not show fidelity to one pine stand or region, but rather wander over many regions

not previously encountered; they settle only in patches of cone-bearing large-seeded conifers. It appears that a significant portion of the population of nutcrackers adopts such an emigrant lifestyle each year (Vander Wall et al. 1981). Emigrating nutcrackers have been observed more than 2,000 km from their traditional breeding range in their search for conifer cones (Fisher and Myres 1979). This nomadic and adaptive food-finding strategy of nutcrackers is advantageous for whitebark pine restoration efforts.

Management Implications of Seed Dispersal by Clark's Nutcracker

Overall, the effectiveness of nutcracker seed dispersal is affected by the decline in whitebark pine. Managers can mitigate the effects of this change and ensure successful whitebark pine restoration by considering aspects of the behavioral ecology of nutcrackers that directly affect their seed disperser effectiveness. For example, as already discussed, nutcrackers and other animals prey on large numbers of seeds in autumn and on young whitebark pine seedlings in spring (Vander Wall and Hutchins 1983; Vander Wall 1992a; Baud 1993; Lorenz and Sullivan, in prep.). Moreover, nutcrackers readily transport whitebark pine seeds to lower elevation forests for caching, and they place a large proportion of seeds in sites unsuitable for seed germination and seedling maturation (Lorenz 2007). Cache-site selection is affected by multiple and complex factors: migratory status, home range composition, the proximity of cache sites to home ranges, and winter snow pack (Lorenz 2007; Lorenz and Sullivan, in prep.). Rather than using direct seeding, whitebark pine should be reintroduced into the wild as seedlings that are old enough to escape predation by animals. It is also important that managers not attempt to mimic nutcracker cache-site preferences when planting seedlings in restoration sites. Rather, managers should select microsites for planting seedlings that are known to increase seedling survival in experimental settings; seedlings should be planted in protected, moist, and partially shaded microsites (Scott and McCaughey 2006).

Managers should also bear in mind that stand treatments that hypothetically encourage nutcracker caching, such as creating forest openings and burned patches (Keane and Arno 2001), may not be effective. Mellman-Brown (2005) found that the spatial distribution of whitebark pine seedlings did not appear to be correlated with nutcracker caching patterns but was associated instead with microsite conditions that favored seed germination and seedling survival. Nutcrackers place caches deliberately on many scales and it appears that first-order selection for cache sites is done on a landscape scale; the selection of a patch or microsite for caching is made only after a larger-scale selection process. Nutcrackers have complex reasons for choosing microsites for caches and they likely evolved cache selection strategies to make it unlikely for any one disturbance event or pilfering animal to wipe out an individual's personal caches. It also makes it less likely that nutcrackers would be affected in their caching decisions by small scale changes such as the creation of clearings in forests. Moreover, because nutcrackers are highly effective seed predators when whitebark pine seeds are germinating, silvicultural techniques to encourage seed caching do not necessarily cause an increase in whitebark pine seedling establishment.

GENETICS

A key component of the Pacific Northwest Region whitebark pine restoration program will be planting seed or seedlings for reforestation of disturbed sites. Movement of seed away from its source of collection increases the risk of maladaptation, which could lead to reduced growth and survival (Campbell 1979). Seed transfer should be guided by natural levels of genetic variation and should take into account the adaptation of populations to their local environment and to potential changes due to global warming. Current predictions of future climate change may complicate seed transfer because it may be advisable to balance suitability of individuals to the current environment, while maintaining a level of adaptability that will ensure that these individuals will be not be

maladapted to future environments. Understanding the genetic structure of a species is crucial in evaluating the conservation of genetic resources and predicting the possible effects of climate change (St. Clair et al. 2005).

Genetic Variation

Whether animal, herbaceous plant, or tree, an individual's genetic makeup, in interaction with its environment, determines the amount of variation in measurable characters (quantitative traits) such as growth, survival, tolerance to biotic and abiotic stress, and disease resistance. Environmental conditions vary widely both geographically and seasonally, and from year to year; so, too, genetic variation is found both among individuals at a particular location, and among groups of individuals at different locations. Genetic variation is important because it provides the raw materials for adaptation to changes in an individual's environment. The amount and structure (the partitioning of variation among individuals within a stand and among different stands) of genetic variation are influenced by gene flow, mutation, genetic drift, selection, and other forces. Management activities can simulate some of these natural forces; therefore, knowledge of the existing genetic structure is important to ensure that these activities do not affect genetic diversity in an undesirable way in the resulting stand.

Genetic Testing

Genetic variation and population structure are assessed in two ways: with molecular markers and quantitative traits.

Molecular markers include subtle differences in enzymes that can be quantified with gel electrophoresis (allozymes) and differences in DNA sequence fragments. DNA fragments used as markers are often in sections of DNA that do not control a specific gene (non-coding) and therefore are not acted upon by natural selection (they are selectively neutral). Thus, while they are useful to identify distinct

breeding units of familial relationships, the differences do not imply differences in adaptation. To determine adaptation, other methods must be used. Allozymes have traditionally been considered selectively neutral; however, because these enzymes often catalyze metabolic processes, it has been argued that these markers are not truly immune to the forces of selection (or at least not all of them). Thus, allozymes also reflect familial relationships, but it is unclear to what degree they reflect adaptation.

Quantitative traits (such as growth, survival, biomass production, and biotic and abiotic stress tolerance) are generally considered better indicators of adaptation and are measured on trees growing in the field (usually in seedling common gardens or field test sites). In these types of tests, individuals from multiple geographic origins are grown together in the same environment. Differences in quantitative traits usually reflect the level of adaptation of a particular population to its local environment and often are related to geographic (latitude, longitude, elevation, distance from the coast) and climatic (temperature, rainfall, growing season length) variables.

Genetic differences among populations (genetic differentiation) that illustrate the genetic structure of a species can be estimated by using both molecular markers and quantitative traits. In most studies where the level of genetic differentiation determined by both types of tests has been compared, differentiation is usually greater when measured by quantitative traits. Since these traits are subject to the effects of natural selection, while molecular markers are usually not, the difference between these measures of genetic differentiation) is often taken as evidence of natural selection resulting in local adaptation.

Genetics of Whitebark Pine

Summary

Studies have shown that the multi-stemmed growth structure of whitebark pine is due to the caching of seeds by the Clark's nutcracker. Using molecular markers, it has been determined that often the stems in these clumps represent more than one genetically distinct individual, with each one arising from a different seed. In general, based on molecular markers, levels of genetic diversity in whitebark pine are comparable to other stone pine species; however, whitebark pine appears to have lower levels of genetic differences among stands than winddispersed pines do. Although whitebark pine stands are not differentiated genetically within a geographic region, populations in the northern (western British Columbia), eastern (Rocky Mountains), and southern regions of the species range (Oregon and California) are genetically distinct. A common result in studies of genetic diversity of whitebark pine is that it commonly experiences inbreeding (selfing, or mating among relatives).

While studies using molecular markers have shown low levels of genetic differentiation, studies using measured traits generally have found considerably



Individual stems within clumps are often related due to nutcracker caching.

more genetic variation and moderate to high levels of population differentiation. The traits studied include cold injury, blister rust resistance, growth, and phenology. Winter temperature appears to be an important climatic determinant driving adaptation of populations to their local environment, and combined with data on population differentiation, has been used to determine guidelines for movement of seed for restoration or reforestation efforts.

Molecular Markers

Genetic variation of whitebark pine has been assessed in several studies using neutral molecular markers at scales ranging from a single watershed to most of its range. Most of these studies used allozymes, but in recent years, newly available DNA markers have been used to refine the knowledge of whitebark pine genetic structure. Caching of seeds by the Clark's nutcracker was first implicated as the cause of the multi-stemmed growth form of whitebark pine in the early 1980s (Lanner 1982, Tomback 1982). The effect of seed dispersal by birds on genetic structure of whitebark pine populations was studied by Furnier et al. (1987), using allozymes. They found more than two genetically distinct individuals in 23 of 35 multistemed clumps, indicating that these stems had arisen from different seeds. They also found that individual stems within clumps are often related, presumably because multiple seeds from the same tree or even the same cone were cached together. While stems within clumps were often related, there was little genetic structure among clumps, with the distance between clumps unrelated to how closely clumps are related.

These results were supported by a study of fine-scale genetic structure also using allozymes, in the eastern Sierra Nevadas (Rogers et al. 1999). Genetic differentiation was assessed among three hierarchical scales: among adjacent watersheds, between upper and lower elevations within a watershed, and within krummholz thickets and clumps. Little differentiation was found among watersheds ($F_{\rm ST}=0.004$) (see table 3 for definition), but differentiation between elevations was moderate ($F_{\rm ST}=0.051$) and within thickets of clumps was strong ($F_{\rm ST}=0.334$). Individuals within

krummholz thickets often shared one or both parents, most likely because of the seed-caching behavior of the Clark's nutcracker.

Several allozyme studies assessing genetic variation and differentiation at varying scales, are summarized in table 3. These studies found that levels of whitebark pine genetic diversity (expected heterozygosity) was within the range of other stone pines (*Pinus* subsection Cembrae [Politov et al. 1992, Jorgensen and Hamrick 1997]); but somewhat below that of wind-dispersed pines in the subgenus Strobus (0.219)(Ledig 1998, Bruederle et al. 2001). Only about 5.3 percent of the measured genetic variation is due to genetic differences among populations, while the vast majority of variation resides within populations. The estimate of population differentiation for the four other *Cembrae*, species is $F_{ST} = 0.046$ (Goncharenko et al. 1993a, 1993b; Krutovskii et al. 1995; Tani et al. 1996; Potenko and Velikov 1998, 2001; Belokon et al. 2005). Thus, populations of bird-dispersed pines do not appear to be strongly differentiated using putatively neutral molecular markers. Wind-dispersed pines typically have less than 10 percent of their genetic diversity among populations (Ledig 1998).

Additionally, Jorgensen and Hamrick (1997) reported that populations that have colonized

areas covered by Pleistocene glaciers were more differentiated than populations from non-glaciated areas. Populations in the northern (western British Columbia), eastern (Rocky Mountains), and southern regions of the species range (Oregon and California) are differentiated for monoterpenes (Zavarin et al. 1991), allozymes (Yandell 1992), and organelle DNA (Richardson et al., 2002b). All the allozyme studies also reported a deficiency in heterozygosity (F > 0), which most commonly results from inbreeding.

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. Because these rare alleles are distributed among populations rather than within them, these authors stated that 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. Furthermore, because blister rust resistance is likely to be rare, the researchers have noted that conserving this allelic diversity may be crucial to whitebark pine's ability to evolve in response to this evolving pathogen (Hoff et al. 1994, Jorgensen and Hamrick 1997).

| Table 3. Summary of results from whitebark pine allozyme studies | | | | | |
|--|-----------------------|---|--------------------------------------|--|--------------------|
| Reference | Number of populations | Area | Genetic diversity (H _e)* | Population differentiation $(F_{ST} \text{ or } G_{ST})^*$ | Inbreeding (F)* |
| Yandell 1992 | 14 | Southern half of range | 0.204 | 0.088 | 0.064 |
| Jorgensen and Hamrick 1997 | 30 | Entire range except British Columbia | 0.102 | 0.034 | 0.043 |
| Bruederle et al. 1998 | 9 | Greater Yellowstone area | 0.152 | 0.025 | 0.026 |
| Stuart-Smith 1998 | 29 | Canadian Rockies | 0.224 | 0.062 | 0.027 |
| Krakowski et al. 2003 | 17 | British Columbia | 0.257 | 0.061 | 0.168 |
| Bower and Aitken, unpublished | 14 | British Columbia, Idaho, Montana, Oregon | 0.216 | 0.047 | 0.154 |

 $^{^*}H_e$ = heterozygosity expected based on allele frequencies, a measure of genetic diversity; $F_{_{ST}}$ and $G_{_{ST}}$ are measures of population differentiation and range from 0 to 1; F = inbreeding coefficient—if F > 0 this is an indicator of inbreeding, if F < 0 then this can indicate selection against inbreds.

Two studies (Krakowski et al. 2003, Bower and Aitken 2007) have assessed the mating system of whitebark pine, to determine the level of inbreeding it experiences and the resulting effect on quantitative traits. The reduced fitness that typically accompanies an increase in homozygosity observed in progeny from matings among relatives is known as inbreeding depression. From two populations in southern British Columbia, Krakowski et al. (2003) reported an inbreeding rate for whitebark pine of 27 percent, presumably as a result of the growth structure of clumps of related individuals. This rate is considerably higher than most wind-pollinated conifers, which typically have inbreeding rates of less than 10 percent (Ledig 1998). Bower and Aitken (2007) confirmed the inbreeding rate for these populations; however, they reported that inbreeding rates ranged from 2 to 12 percent from five populations in Oregon and Montana. The areas where the Oregon and Montana populations were sampled were not glaciated at the last glacial maximum, so the higher level of inbreeding in the southern British Columbia populations may reflect postglacial colonization patterns and processes.

They also reported little evidence of inbreeding on quantitative traits, with only one trait (biomass) in only one geographic region (southern British Columbia) showing a reduction that was correlated with the level of inbreeding. They calculated a decrease in biomass of 19 percent in this region, if inbred individuals are not removed by natural selection. This level of inbreeding in biomass is within the range reported for other conifers. However, no inbreeding depression was detected in traits that are likely to be of greater adaptive significance such as cold hardiness, phenology, and survival. Therefore, relative to other threats faced by whitebark pine, inbreeding depression does not appear to be of great concern; in fact, a study of the effects of inbreeding and blister rust on genetic diversity showed that more inbred individuals (Bower and Aitken unpublished).

Allozymes also were used to assess the effects of inbreeding and white pine blister rust on genetic

diversity from 14 populations in British Columbia, Idaho, Montana, and Oregon that varied in level of blister rust infection (Bower and Aitken, unpublished manuscript). Estimates of genetic diversity (H_o and H₂) and level of inbreeding (F) were compared by age group (seedlings, young trees, and mature trees) within and across sites. Significant evidence of inbreeding (F>0) was found in all age groups. When sites were stratified by level of blister rust infection, differences in inbreeding and genetic diversity among cohorts were significant only when level of infection was low. A significant negative association was found between level of blister rust infection and diversity in the mature cohort, which suggests that inbred individuals appear to have a slight advantage on sites where the level of blister rust is high, possibly owing to recessive genes for blister rust resistance. Inheritance of resistance mechanisms needs to be determined, and if recessive resistance genes are found in whitebark pine, some level of inbreeding may help express these resistance mechanisms.

DNA markers have also been used to study population genetic structure and biogeographic patterns of whitebark pine (Richardson et al. 2002a). Microsatellites (tandemly repeated DNA sequences) were used to assess genetic structure from 41 populations that covered most of the species' range. The Richardson study found that populations clustered by genetic similarity into three main groups: Sierra Nevada; Yellowstone; and all others (northern Cascades, N. Idaho, central Idaho, and S. Oregon); the level of genetic differentiation (0.046) among these three groups was similar to the values reported from the allozyme studies. Based on the geographic patterns observed with the DNA markers, the authors inferred three glacial refugia, in southern Oregon, central Idaho, and the Yellowstone area, with a subsequent post-glacial colonization route northward into Canada and a secondary contact zone between the Oregon and Idaho populations in the Washington Cascades. This probable secondary contact zone was confirmed with a finer scale sampling study at the location of the proposed contact zone (Richardson et al. 2002b)

Quantitative Traits

Because studies of presumably neutral molecular markers do not reflect the effects of selection, they are not sufficient by themselves to adequately describe genetic variation for the purposes of designing seed transfer guidelines.

Only a few studies have assessed genetic variation in quantitative traits such as cold hardiness, growth, phenology, stem form, and disease resistance. The first published study illustrated considerable variation in cold hardiness (measured as the index of injury) (Bower and Aitken 2006). These researchers found that the level of cold hardiness varied throughout the year from below -70° F (-57° C) in the winter to -9° F (23 ° C) in the summer. Acclimation and deacclimation to cold occurred rapidly over a period of 2 to 3 weeks in the fall and spring, respectively; however, even during the period of active shoot elongation, whitebark pine showed greater hardiness to cold than most conifers. Geographic regions differed in cold hardiness in all seasons except in winter. Interior and northern sources were higher and California lower in hardiness the fall, with opposite patterns in the spring. The degree to which spring and fall cold hardiness traits are passed from parent to offspring (heritability) was low to moderate for both traits ($h^2 = 0.18$ and 0.28, for spring and fall, respectively), and fall cold hardiness was significantly correlated with winter temperature of the parental environment.

Mahalovich et al. (2006) also found significant differences among sources for spring cold injury, as well as height growth and blister rust resistance in the northern U.S. Rocky Mountains. In general, cold hardiness and rust resistance showed opposite geographic patterns, with sources in the northwest having higher rust resistance and lower cold hardiness, and southeastern sources having lower rust resistance and higher cold hardiness. Tentative fine-scale seed zones for this area were delineated by Mahalovich and Hoff (2000) and Mahalovich and Dickerson (2004), and the degree of variability reported in this study support these seed zones.

Hamlin et al. (2007) assessed timing and amount of growth, and stem form of Washington and Oregon sources. They found significant differences in mean provenance heights in multiple measurement periods, with the northwestern provenances being tallest and eastern and southern provenances being shorter. There was also significant family variability in each growth period, and heritability (h^2) ranged from 0.40 to 0.65. Moderate correlations existed between final height and elevation (-0.46, lesser height with higher elevation), longitude (0.43, greater height with a more western source), and latitude (0.41, greater height with a more northern source). The proportion of growth also differed significantly among provenances at the start and end of the growing season. Provenances from eastern Oregon (Umatilla and Malheur) appear to both initiate and cease growth earlier than provenances from the Cascades (Mt. Rainier, Mt. Hood, Warm Springs, and Crater Lake), as they a higher proportion of growth completion. Families also differed for this trait with heritability ranging from 0.28 to 0.53.

Bower and Aitken (2008) proposed guidelines for seed transfer based on results from a common garden study including seed from northern (British Columbia); Rocky Mountain (eastern Washington, eastern Oregon, Idaho, Montana, and Wyoming); and southern (western Oregon and California) areas. Seedlings from 48 populations were grown in two soil temperature treatments in Vancouver, British Columbia, to assess genetic variation and differentiation in a number of quantitative traits including height increment growth, biomass, root:shoot ratio, date of needle flush, fall and spring cold hardiness, and survival.

Populations differed significantly for all traits except root:shoot ratio and spring cold injury in the ambient treatment. Growth and survival were higher in the cold-soil temperature treatment than in the ambient treatment, and it appeared that the higher soil temperature in the ambient treatment was a stressor to whitebark pine (approximately 8°C during the warmest part of the day), which is adapted to cold, harsh environments. Growth-related traits showed

low levels of genetic differentiation ($0 < Q_{ST} < 0.14$), while traits related to cold adaptation (date of needle flush and fall cold injury) showed moderate to strong differentiation ($0.36 < Q_{ST} < 0.65$). The mean temperature of the coldest month of the source location had the strongest association with the cold adaptation traits, indicating that this appears to be the climatic variable driving local adaptation.

Bower and Aitken reported that the variation they saw in seedling traits generally was in concordance with the variation found earlier in monoterpenes by Zavarin et al. (1991) and in mtDNA by Richardson et al. (2002a). These two studies also found differentiation among the Rocky Mountain, northern, and southern regions, which may indicate some historical effects of isolation, migration, and genetic drift on quantitative genetic structure in addition to the effects of local adaptation.

At a broad scale, populations from higher latitude environments with lower winter temperatures flushed earlier in the spring, experienced less cold injury in the fall, and allocated more biomass to shoots than roots when grown in the common garden than those from milder environments. However, clinal variation that corresponded to climatic gradients varied by region, indicating that local adaptation is driven by selection pressures from different environmental factors in different regions. In the northern regions, growing season length appeared to be important because date of needle flush had a clinal variation associated with frost-free period. In the Rocky Mountain region, annual and seasonal mean temperature appeared to be driving local adaptation; in the southern region, water availability appeared to be the factor associated with population differentiation, because survival and date of needle flush were both associated with rainfall patterns.

Based on their results, Bower and Aitken (2008) proposed seed transfer guidelines:

 Based on local adaptation of date of needle flush, seed can be moved without substantial risk of maladaptation from seed collection site to planting sites differing up to 1.9°C in mean temperature of

- the coldest month in the northern region, and 1.0° C in the Rocky Mountain region.
- These differences in mean temperature of the coldest month correspond to approximately 4.6 degrees latitude or 505 km for the northern region, and 320 m in elevation in the Rocky Mountain region. These distances are based on a 20 percent risk of maladaptation, but in some cases may be too conservative, especially in the face of climate change.
- If blister rust resistance is found, then it may be necessary to move seed farther to take advantage of this resistance. However, this increases the risk of maladaptation and must be weighed against the need for restoration.
- In the southern region, the lack of correspondence between the seedling and climatic traits meant that seed can be freely moved within this region; however, in the absence of further data, it was recommended that movement between mountain ranges be avoided.
- As temperature appeared to be the driving factor in local adaptation, in order to balance adaptation in current and future climates, seed movement should be unidirectional from milder to colder climates within the local temperature envelope to account for predicted warming due to climate change.

Genetic Studies in Washington and Oregon

Four studies examining range-wide variation in genetic markers of whitebark pine have included samples from Washington and/or Oregon. Of the 30 sites studied by Jorgensen and Hamrick (1997), 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). In two studies, Richardson et al. (2002a, 2002b) included 8 sample sites in Washington (Chinook Pass, Washington Pass, Fox Mt. Pass, Rock Mt., Mission Ridge, Manastash Ridge, Ravens Roost, and Potato Hill) and 4 sites in Oregon (Brown Mt., 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.

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. 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) using isozymes. In contrast, Krakowski et al. (2003) reported expected

heterozygosity of 0.257 in the species overall and 0.260 in one population sampled from Washington with isozymes, which are midrange for pine species (Jorgensen and Hamrick 1997, Bruederle et al. 2001). Richardson et al. (2002a) found very high values for gene diversity, the haploid equivalent of expected heterozygosity using chloroplast (cp) DNA. Gene diversity was 0.928 for the northern Cascades and 0.915 for southern Oregon.

PART 2: WHITEBARK PINE ASSESSMENT AND STRATEGY FOR THE PACIFIC NORTHWEST REGION

An Ecoregion-based Assessment

The Approach

In this section we present the results of an ecoregion-based assessment of the status of whitebark pine on national forests in the Pacific Northwest. This assessment is the culmination of the Pacific Northwest Region's regional 4-year program, which was described in the introduction to this strategy. To determine what needed to be done to conserve and restore whitebark pine across the region, we gathered information on the condition of the habitat and the practicality of working in areas that can be remote and difficult to access. The long-term goal of the Forest Service Region 6 whitebark pine program is to sustain a network of viable populations of whitebark and associated species throughout the Pacific Northwest.

We were inspired to take an ecoregion-based approach by the framework to ecoregional planning used by The Nature Conservancy and the World Wildlife Fund (Groves 2003, Dinerstein et al. 2000). Typically this process is applied to an ecoregion, which is defined as:

...a relatively large unit of land or water that contains a distinct assemblage of natural communities sharing a large majority of species, dynamics, and environmental conditions.

A terrestrial ecoregion is characterized by a dominant vegetation type, which is widely distributed—although not universally present—in the region and gives a unifying character to it.

Because the dominant plant species provide most of the physical structure of terrestrial ecosystems, communities of animals also tend to have a unity or characteristic expression throughout the region (Dinerstein et al. 2000).

Ecoregion-based analysis has been applied to ecoregions such as the Great Basin in Nevada (Nachlinger et al. 2001) and the Chihuahuan Desert of Arizona, New Mexico, Texas, and Mexico (Dinerstein et al. 2001). The components of this process include:

- · Conduct an ecoregion-based assessment.
- Identify overarching threats.
- Select a portfolio of sites for conservation and restoration.
- · Create a biodiversity vision.
- Set long- and short-term conservation goals.
- Prioritize actions to meet conservation goals.

Dinerstein et al. (2000) stress the importance of articulating a biodiversity vision that

incorporates the full range of biological features, how they are currently distributed, how they may need to be restored, and how to safeguard them over the long term. A biodiversity vision is essential because it helps us to move beyond a business-as-usual approach to conservation.

The end result is a site-based conservation blueprint. Our approach also includes a population-based focus in that we have a genetic restoration program for the development of blister rust-resistant material (see the Genetic Restoration Program section, later in this document).

This analysis to restricted to national forests because this is the Forest Service's area of responsibility and influence. We did not analyze the population status of the animal species that are dependent on or associated with whitebark pine, but rather assume that increasing the habitat will benefit species such as grizzly bears and lynx.

Gathering Data

National forest personnel compiled information on the extent and condition of whitebark pine habitat. More than 20 individuals across the region were involved and are listed as contributors to this strategy; theirs was no small task. The compilation included consultation with wilderness specialists, timber planners, ecologists, botanists, and wildlife biologists; it also included sorting through personal accounts from alpine recreation enthusiasts.

We divided the region into nine subregions. These were originally developed as seed zones for the genetic restoration program but also worked well as the first scale for analysis (figs. 4a and 4b). Seed zones were then divided into 30 smaller conservation areas. The development of the seed zone and conservation area system is described in the Genetic Restoration Program section.

Conservation area maps were provided to each forest contributor for review. Suitable habitat was originally mapped with the aid of GIS by using elevation, aspect, plant association data, and satellite imagery vegetation classifications (see the Range, Distribution, and Abundance section in part 1 of this document). Sites with documented whitebark pine presence were plotted. Recent fires (within the past 50 years) greater than 40 ha (100 ac) were mapped; mountain pine beetle activity centers (between 2004 and 2006) also were mapped by using annual regional aerial survey data. Blister rust infection rates were plotted. The reviewers adjusted the suitable habitat boundaries based on local knowledge; unsuitable habitat was removed.

The next task was to divide each conservation area into one to eight management units based on geographic features, whether the unit is in a designated wilderness area or not, and fire history (see appendix 1 for maps). Habitat in designated wilderness requires special consideration (see box).

The reviewers then compiled information on the condition of the habitat, and they described the

access (distance by roads and trails, and existence of helispots) for each management unit. Complete data tables can be found in appendix 2, which includes such information as:

- Blister rust infection levels;
- Fire history;
- Mountain pine beetle level of activity and extent of mortality;
- Presence of mature cone-bearing trees;
- Evidence of seedling establishment;
- Cone-collection history;
- Availability of seed for planting;
- Where confirmed blister rust resistant trees exist;
- What, if any, inventory, planting, or thinning had been done;
- Condition of adjacent lodgepole pine habitat; and
- Opportunities for planting, thinning, and pruning.

For many areas, no information was available other than what could be extrapolated from the maps and from local knowledge of other locations in the conservation area. Frequently, the reviewers commented that the extent and condition of whitebark pine was unknown.

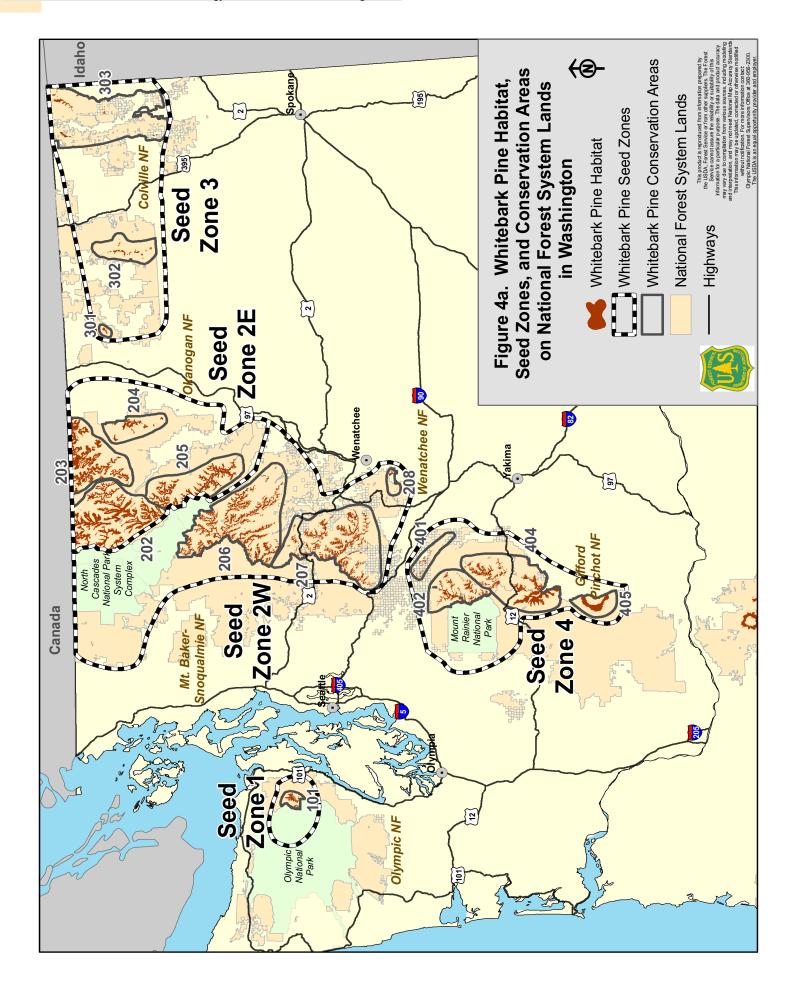
Once the data tables were completed, the information was consolidated so that restoration activities could be assigned to each unit. This consolidated information is summarized in the proposed action summary table for each conservation

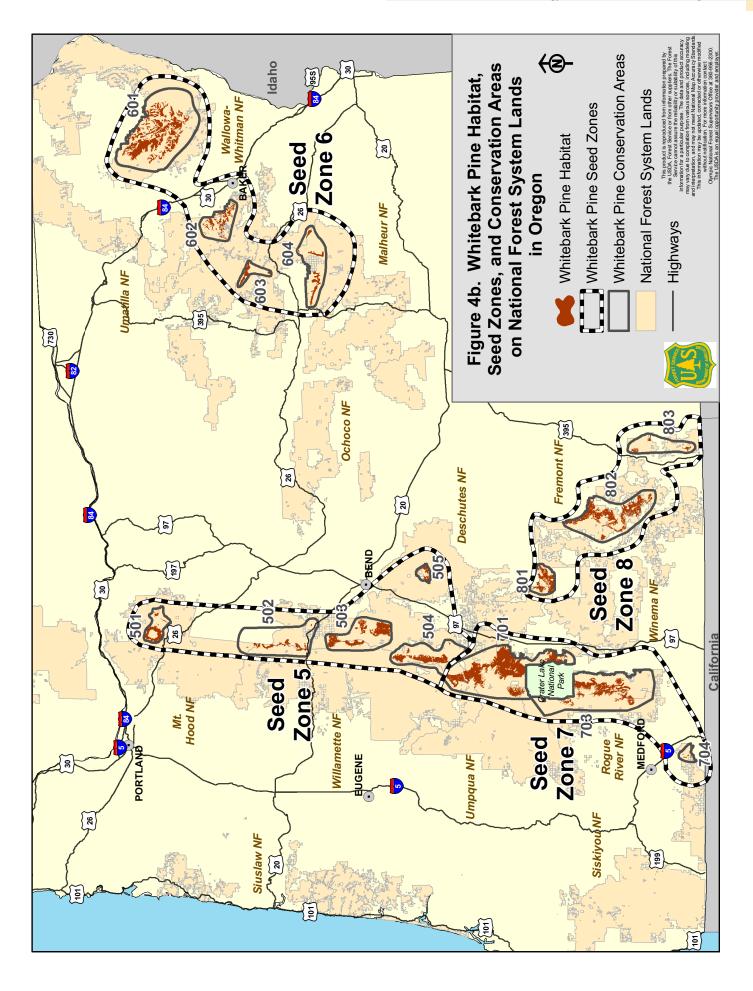
WHITEBARK PINE AND WILDERNESS

A large percentage of the whitebark pine habitat on National Forest System lands in Washington and Oregon is located in congressionally designated wilderness. Generally, management of ecosystem processes in designated wilderness uses a non-manipulative approach with the goal to allow for the free play of natural processes. However when a non-native organism (such as white pine blister rust) or some other anthropogenic factor (such as global warming) alters ecological processes, some of the restrictions may need to be revisited to restore natural processes.

The Wilderness Act of 1964 speaks to "preserving and protecting natural conditions," and defines wilderness as "an area where the earth and its community of life are untrammeled by man." Untrammeled, in this context, means unconstrained or unmanipulated. In some instances, allowing for unmanipulated conditions, such as allowing a river to seek its own channel, preserves the natural process. But in other instances, the natural process has the potential to be so disrupted that an intervention (such as treating noxious weeds) may need to be considered.

Whitebark pine restoration activities being considered for designated wilderness areas would go through a deliberative process using the Minimum Requirement Decision Guide (www.wilderness.net). The guide leads managers through a process to determine whether the action is necessary in designated wilderness areas, and if so, how the project can be designed to be effective but have the least impact on wilderness character. NEPA compliance is also part of this process.





area in appendix 1. Forest personnel used their professional judgment to assign proposed actions to management units by considering the complex interactions among fire, mountain pine beetle activity, blister rust severity, the size of the area, stand age, competition from other conifer species, and reproductive capability of the whitebark pine. It also involved looking at the logistics of getting to an area and the existence of any special management designations (such as designated wilderness or research natural areas) and potential benefit versus cost.

One or more of the following proposed actions were assigned to each management unit:

- Safeguard habitat—Conserve/safeguard from fire (both wild and prescribed). These units will be included in fire and land management plan maps. This action was only assigned to designated wilderness areas, which do not require restoration.
- **2.** Collect cones—Collect cones from mature whitebark pine stands with high potential for cone production.
- **3. Restore**—Plant seed or seedlings, thin for conifer release, and/or prune. Included in this category are units that have burned or have high mortality due to mountain pine beetle infestation. If a stand represents a unique ecological or aesthetic resource (say, at a popular ski area or campground), then pruning branches with blister rust cankers might be a good tool to retain live trees on the landscape, increase the stand's conebearing and regenerative potential, and provide ongoing recruitment of young trees as material for natural selection for blister rust resistance. Pruning may also be beneficial to protect individual high-value trees, such as blister rust resistant candidate trees and trees that are important local seed sources.
- **4. Survey condition**—Survey to determine if whitebark pine is present, to record the general stand condition, and to determine what actions, if any, are needed.
- **5.** Survey seed trees—Survey to determine if conebearing trees are present.
- **6.** No action—Consider a combination of several factors that would indicate this unit is a low priority compared to the others in the conservation area. For

example, units with poor access, marginal habitat, and no need for planting or thinning.

Another consideration in assigning priority actions was the distribution of seed collection sites within each conservation area and seed zone. Are collection sites well-distributed? If not, where are opportunities for collection that more evenly distribute sites across the conservation area?

Continuing to collect seed from established collection sites and identification of new collection sites (the action called "Survey – seed trees") is critical because of the poor distribution of established collection sites and the vulnerability of cone-bearing trees to blister rust, fire, and mountain pine beetle attack throughout most of the region. The action called "Safeguard habitat" was listed for all designated wilderness areas to emphasize the need to protect these areas from stand-replacing fires.

For areas where no local knowledge of whitebark pine was available, units were assigned a proposed action of "Survey – condition." When a unit had a combination of characteristics that made it a very low priority for any restoration activity, it was assigned "No action."

For each conservation area, the top priority units for planting and/or thinning and surveys, either for seed trees or condition, were identified. These are marked by a double asterisk in the proposed action summary tables in appendix 1. Cone collection will be opportunistic and dependent on the size and distribution of the cone crop in any given year, so prioritization for this activity is not necessary.

Assessment Results

This section summarizes by seed zone the state of knowledge; impacts of fire, mountain pine beetle, and blister rust on whitebark pine communities; seed needs and potential for cone collection; and restoration opportunities. The 30 conservation areas and the management units within them vary greatly in whitebark pine distribution and status. Maps and profiles of each management unit are provided in appendix 1, and more details can be found in appendix 2.

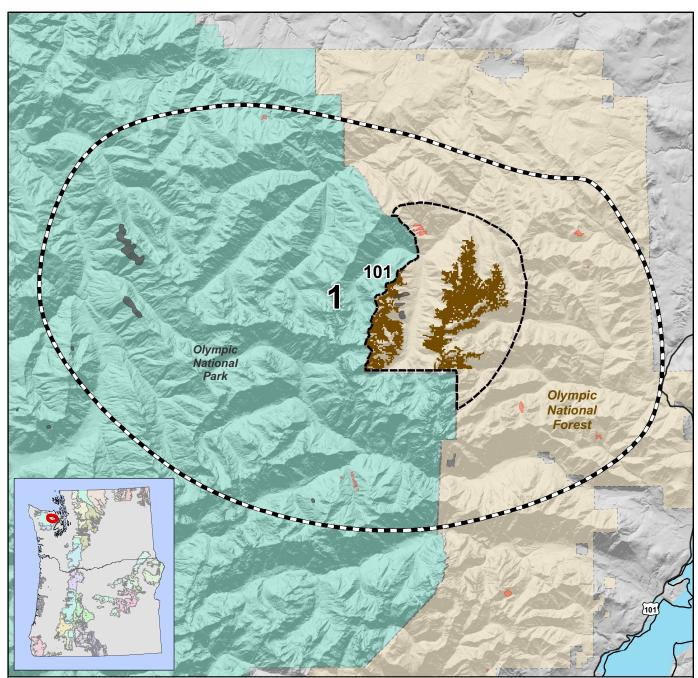
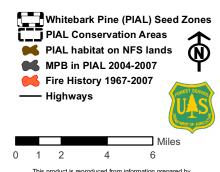


Figure 5. Seed Zone 1: Olympic Peninsula, Washington

This zone is located in northwest Washington on the Olympic Peninsula. It has two management units in one conservation area (101) on the Olympic National Forest. Whitebark pine also occurs on adjacent ridges in the Olympic National Park. All habitat is in designated wilderness. Blister rust infection rate in the seed zone was recorded at 5 to 69 percent There has been little recent mountain pine beetle activity and no documented recent fires. Access is by trail only. Cone collection is needed throughout the conservation area. Status of the whitebark pine community in the western half of the conservation area is unknown.



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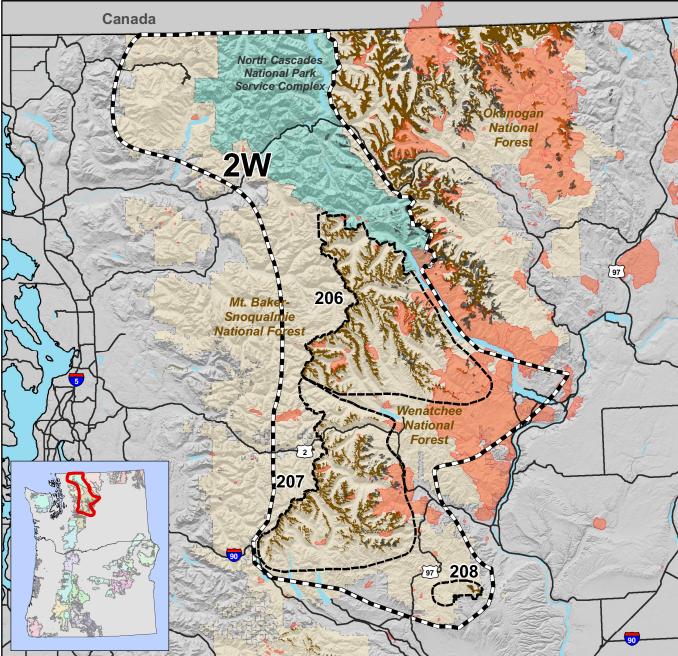
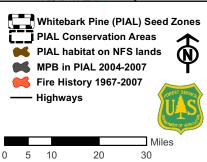


Figure 6. Seed Zone 2W: North Cascades, Washington

This zone includes the North Cascades National Park and the northern part of the Wenatchee National Forest. A few scattered trees occur on the Mt. Baker-Snoqualmie National Forest. Whitebark pine habitat in this zone is in wilderness on the west slope (to the crest of the Cascades), and outside of wilderness on the east slope. Some units are very remote with poor access, while others may be accessed by roads. Blister rust infection rate was recorded at 0 to 53 percent. Although there have been large fires in this zone, the number of acres of whitebark pine habitat burned has been small (conservation areas 206 and 207). Mountain pine beetle activity is very high. Seed collection sites are accessible throughout the zone. Status of whitebark pine is unknown in many areas, and surveys for condition are needed in units across the zone. Planting and tree thinning are restoration needs in conservation area 206. Surveys are needed to assess extent of mortality due to mountain pine beetle and determine potential for planting in conservation area 208.



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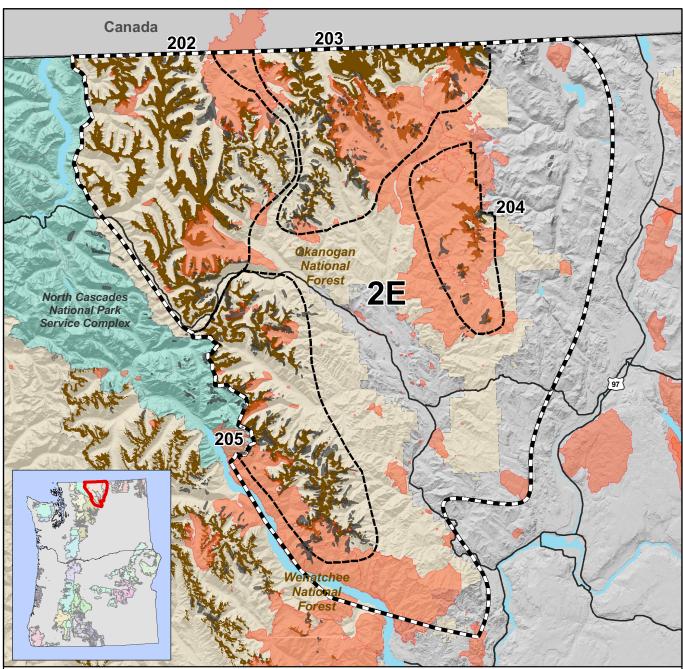
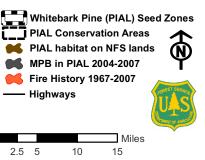


Figure 7. Seed Zone 2E: North Cascades, Washington

Part of the North Cascades Grizzly Bear Recovery Area, this zone includes the western part of the Okanogan National Forest and a small portion of the Wenatchee National Forest north of Lake Chelan. There are 25 management units distributed across four conservation areas. Whitebark pine habitat is in both designated wilderness and non-wilderness. There is some adjacent habitat in British Columbia to the north, and in the Loomis State Forest to the east. Blister rust infection rate was recorded as 11 to 77 percent. Fire has destroyed large areas, and mortality due to mountain pine beetle is high; planting is indicated in conservation areas 202, 203, 204, and 205. Access varies from good to very poor. Presence and status of PIAL are unknown in many areas, and surveys for condition are needed in at least one unit in each conservation area. There are good areas for cone collection in the seed zone, although surveys are needed to select seed trees.



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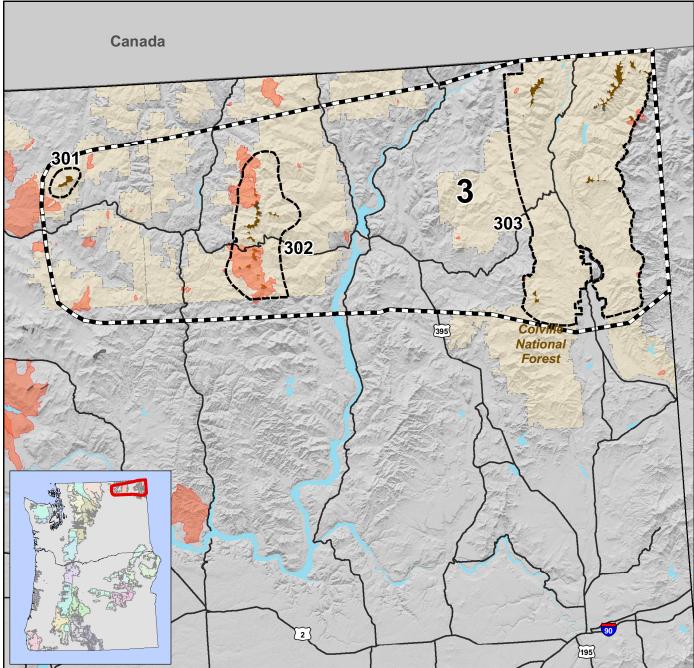
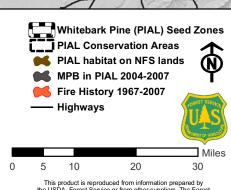


Figure 8. Seed Zone 3: Northeast Washington

Three conservation areas separated by at least 30 miles are located on the Okanogan and Colville National Forests. Most whitebark pine habitat is outside of designated wilderness except for the northeast corner of conservation area 303. Round Top Mt., also in conservation area 303, is a designated research natural area. Most habitat in this seed zone is in small patches on isolated peaks and ridges. Blister rust infection rate was recorded at 18 to 35 percent. Mountain pine beetle activity is high. Post-fire planting is needed to regenerate conservation areas 302 and 303; these are established cone collection areas but additional seed is needed for sowing. Tree thinning also is needed in both these areas to reduce competition. Surveys are needed in conservation area 301 to determine status, condition, and restoration needs.



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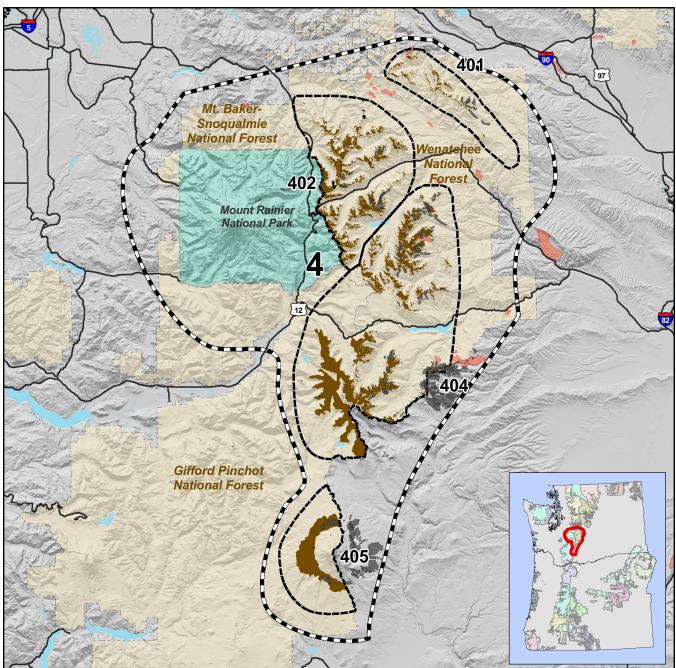
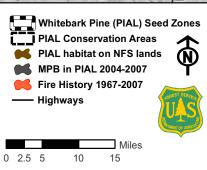


Figure 9. Seed Zone 4: South Cascades, Washington

There are four conservation areas in this zone, which includes Mt. Rainier National Park and parts of the Mt Baker-Snoqualmie, Wenatchee, and Gifford Pinchot National Forests. Blister rust infection rate was 14 to 100 percent, with the highest levels recorded at the south end of the Mt. Adams Wilderness in conservation area 405. Surveys are needed in all areas to determine condition of habitat and mountain pine beetle activity. Mountain pine beetle mortality has been recorded in several units of conservation area 404, and planting may be needed. There are many cone-collection sites throughout the zone. Access is good by road and trail throughout most of the seed zone. Whitebark pine habitat also occurs east of national forest system boundaries on Yakama Indian Nation land and on state forest land.



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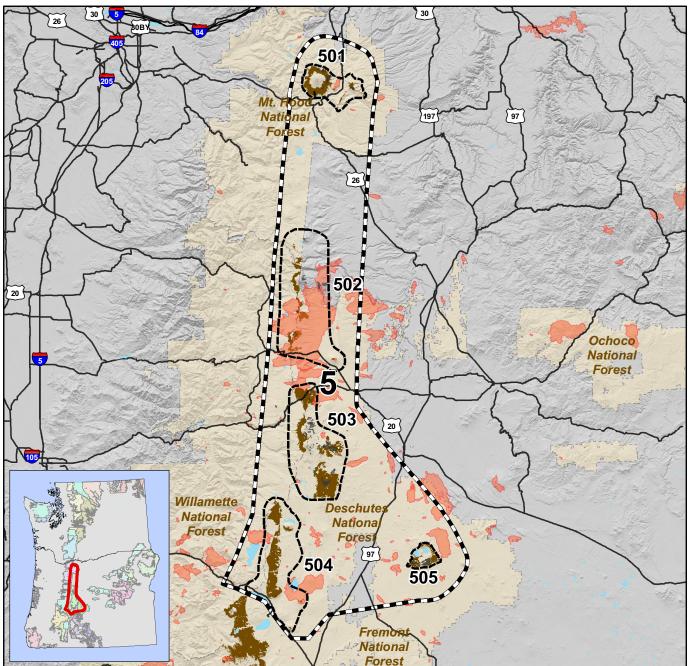
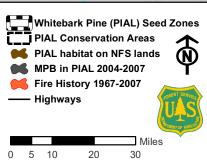


Figure 10. Seed Zone 5: North Cascades, Oregon

A "ring" of whitebark pine habitat on Mt. Hood (conservation area 501) and an isolated area on Newberry Crater (conservation area 505) are two unique features of this zone. On the Willamette and Deschutes National Forests, whitebark pine habitat occupies a narrow band along the Cascade Crest. Mountain pine beetle are active, and blister rust infection rate varied from 5 to 100 percent. In 2003, fire burned through much of the habitat in conservation area 502. Although there are several areas that need to be surveyed, there are well-documented sites in each conservation area that need to be planted. Seed is available and road access to these areas is good. There are also tree thinning opportunities in conservation areas 501 and 504 and pruning in conservation area 501.



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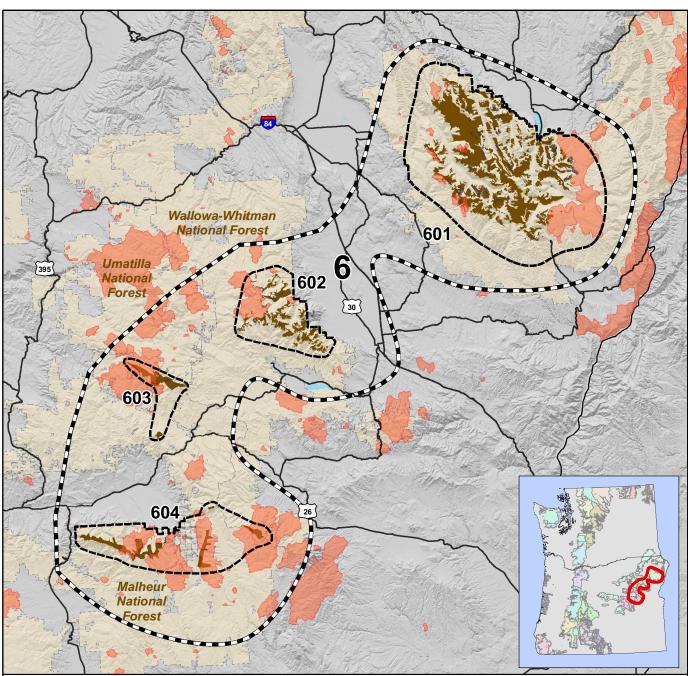
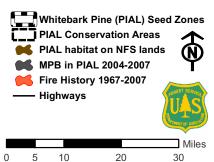


Figure 11. Seed Zone 6: Blue Mountains, Eastern Oregon

The Eagle Cap Wilderness, located on the Wallowa-Whitman National Forest (conservation area 601), provides the largest continuous whitebark pine habitat in this seed zone. Post-fire surveys are needed to determine planting needs in several areas. This also applies to conservation area 604 on the Malheur National Forest. Planting and tree thinning are proposed in conservation area 602 (also on the Wallowa-Whitman) and in conservation area 603 on the Umatilla and Malheur National Forests. Mountain pine beetle activity is high in all areas except in conservation area 604, and has caused mortality that requires replacement planting. Blister rust infection is moderate to high and was recorded at 49 percent at Vinegar Hill in conservation area 603.



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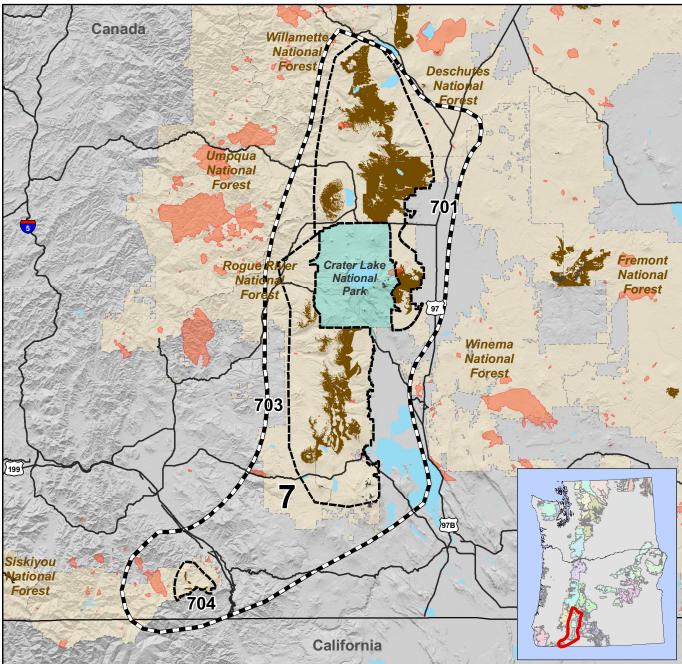
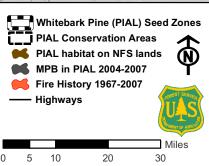


Figure 12. Seed Zone 7: South Cascades, Oregon

Habitat in this zone is found on the Willamette, Deschutes, Umpqua, Winema, and Rogue River National Forests and in Crater Lake National Park. There have been no recent large fires in any of the units and very little mountain pine beetle activity. Reported blister rust infection rates ranged from 24 to 45 percent. Road access is good in most units. Surveys to determine whitebark pine habitat extent and condition are needed in eight of the units in conservation areas 701 and 703. A number of units have established cone collection sites. Conservation area 704 in the Mt. Ashland watershed is geographically isolated from the rest of the seed zone.



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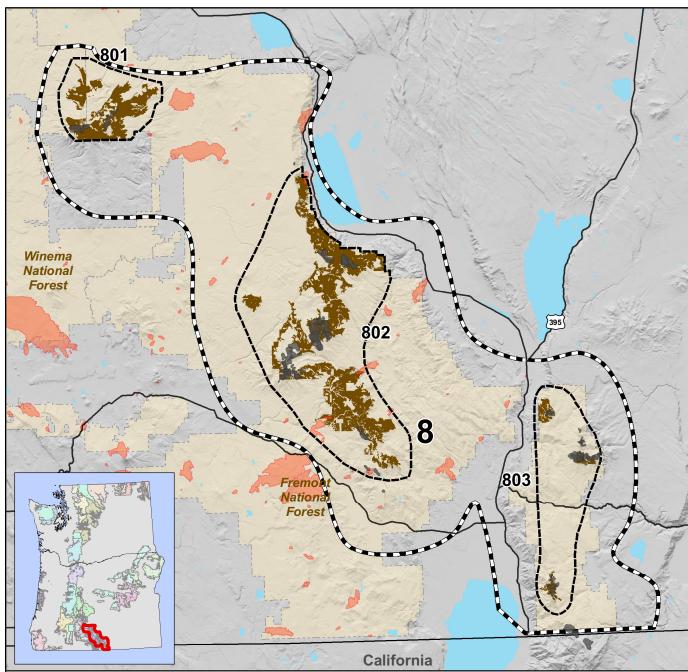
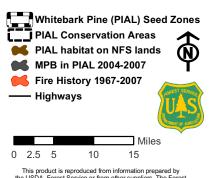


Figure 13. Seed Zone 8: Eastern Cascades Slopes, Oregon

Most whitebark pine habitat in this zone is on the Fremont National Forest. The three conservation areas are separated by more than 32 km (20 mi). Most habitat is outside of designated wilderness. Recent fires have burned in portions of whitebark pine habitat in conservation area 802. Mountain pine beetle activity has been very high in conservation areas 802 and 803. For these reasons, planting is needed in all units of conservation area 803 and in the north section of conservation area 802. Tree thinning in both units of conservation area 801 would reduce potential losses due to fire and to mountain pine beetle, which has not reached this area to date. No blister rust infection has been found in conservation areas 801 and 802; conservation area 803 has not been surveyed for blister rust. Road access is good for most areas.



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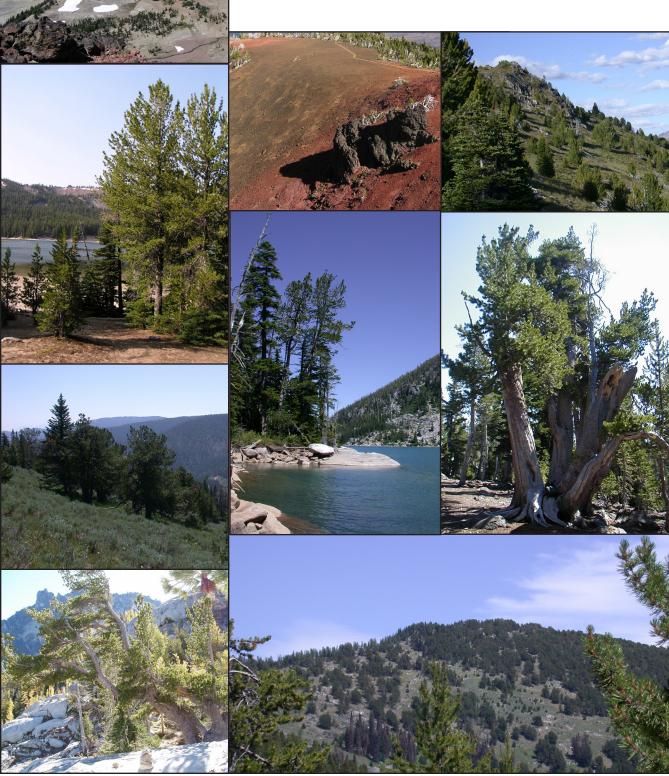
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Whitebark pine is found in a wide variety of high-evelation habitats in Washington and Oregon.

All photos U.S. Forest Service (Jamie Cannon, Chris Jensen, Mike Roantree, Robin Shoal) unless otherwise noted. Lower 3 photos on page 2 by Michele Laubenheimer, U.S. National Park Service.





The Work Ahead: Proposed Actions

A look at the proposed actions across the region clearly shows the need for a restoration program in the next 5 years (table 4). Action descriptions are given in the introduction to appendix 1. See appendices 1 and 2 for the rationale behind recommendations made for each management unit.

Planting is indicated in every conservation area except for the Olympic Peninsula. At present, all whitebark pine seed available for sowing is from trees phenotypically selected for blister rust resistance; only a small number of trees have been through rust resistance screening. Nevertheless, land managers agree that reforesting stands that have been destroyed by high-severity fire or mountain pine beetle infestation must be done soon and cannot wait for rust resistance screening to be completed. Moreover, although Clark's Nutcrackers may cache in these areas opened by fire or beetles, nutcracker "planting" alone will not be sufficient to achieve stand replacement (see Seed Fate section earlier in this document).



Planting whitebark pine seedlings on a heavily trodden recreation site.

Table 4. Proposed actions across conservation areas* Restore Survey - seed Survey Safeguard Restore CA habitat **Collect cones** No action plant Restore - thin - prune trees condition 101 202 203 204 205 206 207 208 301 302 Χ Х 303 401 402 404 405 501 502 503 504 505 601 602 Х Χ 603 604 701 Χ 703 704 801 802

^{*} There may be multiple units with the same activity.

Mortality due to blister rust is to be expected when seedlings (either planted or natural) have not been screened for resistance. Early test results indicate that there is variation in resistance among families and that the level of resistance varies across the region (see the Genetic Restoration Program section). Of the families tested, on average, 30 percent have shown rust resistance but the levels of resistance varied by location from as low as 0 percent and as high of 90 percent. This information can be used to estimate the number of trees to plant per acre that will take into account expected mortality. For an in-depth discussion of planting design and other restoration techniques for whitebark pine in the Pacific Northwest, consult Shoal and Aubry (2008).

Tree thinning is indicated in nine conservation areas to reduce competition. In conservation areas 501 and 602, pruning infected limbs is suggested to prolong survival of individual trees for cone collection.

During analysis, it became clear that basic knowledge is lacking for much of the whitebark pine habitat across the region. Surveys (Surveys – condition in table 4) are recommended for 53 management units to verify habitat maps, stand conditions, and what, if any, restoration work is required.

There are ample opportunities to collect cones as indicated by the number of conservation areas checked in table 4. However, some units that appeared to have



Subalpine fir trees girdled as part of a thinning treatment to reduce competition by other conifers in a mixed stand.

potential cone collection will need to be surveyed (Survey – seed trees) to confirm the locations of seed trees.

Setting Priorities

Funding will undoubtedly continue to be very limited; in the next 5 years, our efforts must be focused in units that provide the greatest benefit for the lowest cost. For this reason, we evaluated management units by the criteria described below and ranked the units that need planting and surveys. The top 10 units in each category were then selected (table 5).

Planting

Top priority for planting was given to management units located in grizzly bear habitat. As part of recovery plans for grizzly bears under the Endangered Species Act, all whitebark pine communities in seed zones 2W and 2E are in the Northern Cascades Grizzly Bear Recovery area; conservation area 303 is in the Selkirks Grizzly Bear Recovery Area (Kasworm et al. 2007). Whitebark pine seeds are an important food source for grizzly bears, and restoring habitat for this endangered species is critical. (See Kendall and Arno 1990 and Tomback et al. 2001 for reviews of whitebark pine seed use by grizzly bears.)

Next, one or more management units from the conservation areas outside grizzly bear recovery areas were selected to distribute the planting units across the region. These were chosen from the top priority units in each conservation area, which had been designated during the analysis process and are indicated in appendix 1 by **. Priority was given to management units that are outside designated wilderness areas, easier to access and covering relatively larger areas of habitat. It may seem surprising that logistical rather than biological criteria were used. However, within a conservation area, differences in practical issues such as the time it takes to reach and transverse a unit and economies of scale held greater weight than differences in blister rust infection rate or presence of mountain pine beetle. Also, since all planting is managed by individual ranger districts, it would be impractical to concentrate the planting program in a few conservation areas.

Seed is available for all seed zones, so it was not necessary to use adequate seed on inventory as a selection criterion (see the Genetics Restoration Program section). Of the 33 management units for which planting were recommended, restoration in the 10 units listed in table 5 will be done first.

Surveys

It was also important to select the top priority units to survey for condition, because information from little-known units is crucial to planning for units about which we know very little. Overal, surveys are needed in 53 units across all conservation areas. The top 10 units for surveys for condition (table 6) were selected

based on combination of the following criteria:

- Grizzly bear recovery area,
- · Outside designated wilderness areas,
- · Accessibility, and
- Unit ranked among top 10 for planting.

5-year Targets

The results of this assessment illustrate the extent of degradation of whitebark pine habitat from fire and mountain pine beetle. Also revealed is also a lack of information on stand conditions and even whitebark pine distribution in many units across the region.

| Table 5. Top 10 priority management units for planting | | | | | | |
|--|--------------------|----------------------------|-----------------|----------------------------|---------------------------------|------------------------------|
| Conservation area | Management unit | Grizzly bear recovery area | Accessibility | Planting needed after fire | Planting needed - MBP mortality | Blister rust infection rate* |
| 204 | 5 | Υ | Road | Υ | N | 77 |
| 205 | 5 | Y | Road and Trails | Y | Y | 57 |
| 206 | 4 | Y | Road | Y | Y | 43 |
| 303 | 1 | Υ | Trails only | N | Y | 22 |
| 404 | 3 | N | Road | N | Υ | 56 |
| 501 | 4 | N | Road | N | Y | 47 |
| 503 | 5 | N | Road | N | Y | 50 |
| 504 | 5 | N | Road | Y | N | 35 |
| 603 | 3 | N | Road | N | Υ | 49 |
| 701 | 7 | N | Road | N | Υ | 45 |
| 803 | 1 | N | Road | N | Y | 0** |

^{*} Highest rate recorded in conservation area (Shoal and Aubry 2006; Ward et al. 2006).

^{**}Recorded in conservation areas 801 and 802.

| Table 6. Top 10 priority management units for surveying condition | | | | | | | |
|---|--------------------|----------------------------|-------------------------------------|---------------|----------------------------------|---------------------------------|------------------------------------|
| Conservation area | Management unit | Grizzly bear recovery area | Outside designated wilderness | Accessibility | Planting needed after fire | Planting needed - MBP mortality | Blister rust infection rate* |
| 203 | 3 | Y | N | Trails only | Υ | N | 56 |
| 204 | 4 | Y | Υ | Road | Υ | Υ | 77 |
| 206 | 7 | Y | Υ | Road | Υ | Y | 43 |
| 208 | 2 | Y | Υ | Road | N | Y | 10 |
| 301 | 1 | Y | Υ | Road | N | Y | Unknown |
| 404 | 3 | N | Υ | Road | N | Y | 56 |
| 501 | 8 | N | Υ | Road | N | Υ | 47 |
| 502 | 3 | N | Υ | Road | Υ | N | 80 |
| 603 | 4 | N | Υ | Road | N | Y | 49 |
| 802 | 2 | N | У | Road | Υ | Υ | 0 |

^{*} Highest rate recorded in conservation area (Shoal and Aubry 2006; Ward et al. 2006). Abbreviations used in this table: MPB=mountain pine beetle.

The high rate of blister rust infection and resulting mortality are also of great concern.

The following is a list of actions to be accomplished over the next 5 years as steps to reach the long-term goal: a network of viable populations of whitebark pine throughout the Pacific Northwest with an increase in the level of resistance to blister rust.

Actions

- Collect seed following a regional plan to meet gene conservation, rust resistance screening, and planting objectives.
- Survey all priority management units (table 6).
- Develop and implement a plan to plant priority management units (table 5).
- Continue rust screening program with emphasis on seed zones in grizzly bear recovery areas.
- Develop and implement a plan to treat mountain pine beetle in high risk units.
- Develop an approach for planting in designated wilderness areas that will allow the use of resistant plant material while maintaining wilderness character.
- Develop an approach to mitigate the predicted impacts of climate change.
- Develop monitoring plan(s) to track accomplishments, measure success of actions, provide information and feedback to improve procedures and outcomes of projects, and disseminate information.

Proposed Whitebark Pine Restoration Program, 2009–2013

The most efficient and effective way to meet the 5year targets listed above is through the assignment of a regional whitebark pine program coordinator who can devote the time and attention needed to activities that are best approached from a regional perspective. We estimate that about 6 months per year for the next 5 years would be sufficient for a coordinator to oversee the major objectives of the program including:

- Develop a partnership among land managers (private, federal and state) in the Pacific Northwest to coordinate whitebark pine restoration efforts and share information.
- Coordinate cone collection.
- Assist forest personnel in the implementation of survey and planting programs.
- Assist Dorena program managers in rust resistance screening.
- Assist Forest Health Protection Program entomologists in mountain pine beetle treatment.
- Assist national forest fire specialists in the development wildfire use management plans for whitebark pine stands.
- Manage budget, including grant applications.
- Design and implement ex situ gene conservation seed sampling.
- Develop a restoration plan specifically for designated wilderness areas in partnership with wilderness specialists.
- Produce annual accomplishment reports.
- Coordinate with researchers in the development of key research questions.
- Maintain a website for the exchange of information among whitebark pine researchers and managers.

The coordinator would also implement a monitoring program, which is crucial to measure success and make improvements. The goals of the monitoring program will be to (1) evaluate the effectiveness of restoration and conservation program activities; and (2) assess the status of whitebark pine communities

through the establishment of permanent plots for longterm monitoring of fire activity, stand health, mountain pine beetle activity, and blister rust infection rates and regeneration success.

The authors of this strategy will develop a separate report outlining an 5-year action plan including an annual program of work and a budget proposal. It will include the following elements:

| Activity | Goals and objectives |
|---------------------------------|---|
| Cone collection | Number of sites and trees per site per year |
| Rust resistance screening | Number of families per year |
| Ex situ gene conservation | Number of collections per year |
| Planting | Number of acres per year |
| Thinning | Number of acres per year |
| Pruning | Number of units per year |
| Surveys | Number of units per year |
| Monitoring | Goals and objectives, number of units |
| Mountain pine beetle treatments | Number of trees or acres per year |
| Training | Workshops and publications planned |

GENETIC RESTORATION PROGRAM

The goals of the Pacific Northwest Region's genetic restoration program are to gain an understanding of

Genetic differences among plant populations usually evolve in response to variation in important environmental factors, especially temperature, length of the growing season, and moisture. A continuous change in these parameters from one location to another is known as an environmental gradient, and a continuous genetic change along this gradient is known as a cline. Ideally, seed zones would be determined by knowing how these important environmental factors change across the landscape and how the species adapt to these changes (Randall and Berrang 2002).

the patterns of genetic diversity and adaptation in whitebark pine and to use this knowledge to protect the whitebark pine genetic resource (gene conservation) and to provide rust resistant seed for restoration. White pine blister rust, caused by the introduced pathogenic fungus, *Cronartium ribicola*, has caused infection and mortality in whitebark pine stands through its range in the Pacific Northwest (tables 1 and 2, earlier). As with white pine and sugar pine, increasing the level of rust resistance in whitebark pine is key to the success of this restoration strategy. In order to best deploy rust-resistant seed and create an effective gene conservation program, it is critical to understand the limits to seed movement.

Seed Movement, Seed Zones, and Seed Transfer Guidelines for Whitebark Pine

To have a successful planting program it is crucial to know how far seed can be moved from its source. The greater the area over which seed can be moved, the more efficient and economical a restoration program will be, because there a limited number of rustresistant trees will be found through the resistance testing program. Seed zones divide the range of a tree species into areas where either the environment is fairly similar, or genetic analysis indicates that seed can be moved within the area without loss of adaptation—or a mixture of both factors. Seed zones must be conservative enough to assure adaptation to the local environment and broad enough to be practical. A history of the development of seed zones for native conifers of the Pacific Northwest can be found in Randall and Berrang (2002).

The genetics of whitebark pine was reviewed in part I of this document. We used this information to develop seed zones and seed movement guidelines that will provide a framework for gene conservation plant material collections and seed deployment.

By using a combination of sources of information, we devised nine provisional seed zones for whitebark pine habitat in Washington and Oregon (table 7 and fig. 4). We included Level IV ecoregion designations (U.S. EPA 2007) as one way to note the similarity of environment within each seed zone. Ecoregions are based on an analysis of the spatial patterns and the composition of biotic and abiotic phenomena, which include geology, physiography, vegetation, climate, soils, land use, wildlife distributions, and hydrology (Thorson et al. 2003).

Often it is advisable to restrict seed movement by elevation to reduce the risk of maladaptation. For example, in Washington State the seed zones for Douglas-fir are divided into six 1,000-ft (305-m) elevation bands (Randall and Berrang 2002). However, the results of studies by Mahalovich et al. (2006) and Bower and Aitken (2008), as discussed earlier, indicated that this restriction by elevation is not necessary for whitebark pine.

Seed zones 1, 3, 6, and 8 are presumed to be geographically isolated from other populations given the distance between them; little seed or pollen exchange and therefore little gene flow, is expected to occur between these zones and their nearest neighboring seed zones. After initially delineating one zone for the North Cascades, further analysis of climate data and recently completed genetic analysis of the results of common garden tests indicated that it would be prudent to divide this large area into 2 East and 2 West at the boundary between North Cascades National Park and Wenatchee National Forest and along the Lake Chelan valley. (See the Genetics section for details.)

There is a natural environmental break along Snoqualmie Pass (Interstate 90) that divides the northern and southern Cascades in Washington; we used this natural break as the boundary between seed zones 2W and 4. There are at least 18 miles separating

| Table 7. Seed zones for whitebark pine in Oregon and Washington | | | | | |
|---|---------------------------------|------------|---|-----------------------|--|
| Seed zone | Description | State | National forests and national parks | Ecoregions* | |
| 1 | Olympic Peninsula | Washington | Olympic NP Olympic NF | 77i | |
| 2East | North Cascades | Washington | Okanogan NF west of Hwy 97 Wenatchee NF | 77b, 77c, 77d, 77g | |
| 2West | Central Cascades | Washington | North Cascades NP Wenatchee NF | | |
| 3 | Northeast, Selkirk Mountains | Washington | Okanogan NF east of Hwy 97 Colville NF | 15h, 15x, 15y | |
| 4 | South Cascades | Washington | Mt. Rainier National Park Gifford Pinchot NF | 4b, 4c, 4d | |
| 5 | North Cascades | Oregon | Mt. Hood NF Willamette NF Deschutes NF | 4c, 4d | |
| 6 | Blue Mountains | Oregon | Wallawa-Whitman NF Umatilla NF Malheur NF | 11m | |
| 7 | South Cascades | Oregon | Willamette NF Deschutes Umpqua NF Rogue NF | 4e, 4d | |
| 8 | Eastern Cascades Slopes | Oregon | Fremont NF | 9e 9h | |

^{*} U.S. EPA 2007

Abbreviations used in this table: NP = national park; NF = national forest

these two zones, which is the maximum distance Clark's nutcrackers have been found to transport seeds to cache sites in the Cascades (Lorenz and Sullivan, in prep). The results of genetic analysis also pointed to Snoqualmie Pass as a barrier to whitebark pine seed dispersal (Richardson et al. (2002b).

The range of whitebark pine habitat is much more restricted in the Cascade Mountains of Oregon, where the habitat is often limited to mountain peaks. We therefore divided the Oregon Cascades into two seed zones, 5 and 7, at the Level IV ecoregion boundary between Cascade Crest Montane Forest and the High Southern Cascades Montane Forest. This is a conservative approach based on our expectation that there might be clinal variation in some genetic traits from north to south in the Oregon Cascades.

While seed zones define a geographic area within which seed can be moved with little risk of maladaptation, seed transfer guidelines describe factors that limit seed movement from one place to another. These factors might include distance, elevation, temperature, length of growing season, and moisture, among others.

Seed transfer guidelines are useful in combining individual tree seed collections. At present, many whitebark pine seed lots are being collected, extracted, inventoried, and stored by the tree from which is was collected (table 8). This will allow us to create custom seed lots as new information becomes available on seed transfer guidelines and rust resistances levels and changes in the environment due to climate change.



Germinating whitebark pine seedlings

There are three seed zones within which it would be ideal when simply considering adaptation to the present local environmental conditions to further restrict seed movement. In seed zone 3, there is a considerable distance (29 km [18 mi] or more) between discrete areas of habitat. It would be ideal to restrict seed movement among these areas, although it might not be practical. This same reasoning also applies to seed zone 6; it would be best to not move seed among conservation areas 601, 602/603, and 604, again because of geographical distance. In seed zone 8, the distance between conservation area 801 and 802 is more than 35 km (22 mi), and between conservation area 801 and 802 is about 31 km (19 mi). Similarly, in seed zone 5, conservation areas 501 and 505 are geographically separated from the rest of the seed zone.

However, information on the levels and patterns of blister rust resistance across the landscape and warming trends due to climate change may support broader seed deployment. After careful consideration of the risks and benefits of combining or moving seed from different parts of the range of whitebark pine, it may be decided to use whitebark pine families that show high levels of resistance beyond their seed zone. Also, a portion of seed from a seed zone to the south could also be moved northward in anticipation of climate change. These decisions will be made as results of resistance testing and the development of climate change decision support tools and models to predict future patterns of forest vegetation are developed (Howe 2007, Solomon 2008).

Gene Conservation

Maintenance of genetic diversity is especially important for whitebark pine because of (1) past and potential future losses due to fire, mountain pine beetle, and blister rust; (2) the need to screen a large number of trees to find rust-resistant families; and (3) the pressure the species will undergo from climate change in the future. The following gene conservation issues were noted as critical for the Pacific Northwest at a workshop in 2005 (Goheen et al. 2007):

| Table 8. Seed inventory | | | | | |
|-------------------------|-------------------|---|-------------------------------|---------------------------------------|--------------------------------------|
| Seed zone | Conservation area | National forest | Number of trees (total) | Number of trees with >100 seeds | Total seeds all trees Dec 2006 |
| 1 | 101 | Olympic | 9 | 9 | 5,369 |
| 2 | 202 | Okanogan and Wenatchee | 0 | 0 | 0 |
| 2 | 203 | Okanogan and Wenatchee | 0 | 0 | 0 |
| 2 | 204 | Okanogan and Wenatchee | 10 | 9 | 4,471 |
| 2 | 205 | Okanogan and Wenatchee | 7 | 7 | 2,549 |
| 2 | 206 | Okanogan and Wenatchee | 13 | 13 | 9,112 |
| 2 | 207 | Okanogan and Wenatchee | 0 | 0 | 0 |
| 2 | 208 | Okanogan and Wenatchee | 10 | 10 | 7,202 |
| 3 | 301 | Colville | 0 | 0 | 0 |
| 3 | 302 | Colville | 27 | 10 | 2,676 |
| 3 | 303 | Colville | 19 | 3 | 2,701 |
| 4 | 401 | Okanogan and Wenatchee | 0 | 0 | 0 |
| 4 | 402 | Okanogan and Wenatchee/Mt. Baker-Snoqualmie | 4 | 4 | 3,515 |
| 4 | 404 | Okanogan and Wenatchee/Gifford Pinchot | 8 | 8 | 8,709 |
| 4 | 405 | Gifford Pinchot | 14 | 14 | 10,048 |
| 5 | 501 | Mt. Hood | 20 | 19 | 32,351 |
| 5 | 502 | Mt. Hood/Willamette/Deschutes | 27 | 20 | 24,132 |
| 5 | 503 | Willamette/Deschutes | 29 | 25 | 26,238 |
| 5 | 504 | Willamette/Deschutes | 5 | 5 | 4,989 |
| 5 | 505 | Deschutes | 18 | 17 | 14,380 |
| 6 | 601 | Wallowa-Whitman | 0 | 0 | 0 |
| 6 | 602 | Wallowa-Whitman | 13 | 13 | 13,291 |
| 6 | 603 | Umatilla/Malheur | 49 | 47 | 71,465 |
| 6 | 604 | Malheur | 8 | 8 | 8,363 |
| 7 | 701 | Willamette/Deschutes/Umpqua/Winema | 21 | 11 | 5,908 |
| 7 | 703 | Rogue River-Siskiyou/Winema | 17 | 11 | 9,489 |
| 7 | 704 | Rogue River-Siskiyou | 1 | 0 | 47 |
| 8 | 801 | Fremont-Winema | 0 | 0 | 0 |
| 8 | 802 | Fremont-Winema | 0 | 0 | 0 |
| 8 | 803 | Fremont-Winema | 30 | 22 | 17,145 |

- Strategy for gene conservation throughout its range;
- Gene conservation seed collections (seed banking/ screening);
- Long-term seed storage bank for gene conservation plus viability requirements for longterm seed storage.

Typically, a gene conservation plan focuses on genetic resources in both their original location (*in situ*) and at some other location (*ex situ*) (Lipow et al. 2002). The relative importance of these types of conservation is based on the particular past and present management and life history of the species.

In Situ

For most species, *in situ* conservation is the best solution (Ledig 1988) since it is not necessary to preserve samples of genes.

More than 90 percent of the whitebark pine habitat in the Pacific Northwest is on federally administered land: four national parks and 14 national forests. Most of the habitat on National Forest System land can be thought of as an *in situ* reserve system, with more than 303,500 ha (750,000 acres) in designated wilderness areas. There has been little to no tree harvest or planting of whitebark pine in land allocations outside designated wilderness (about 174,000 ha [430,000 acres]), so these forests can also be considered "in



Robin Shoal, USFS

reserve." Habitat in designated wilderness is well-distributed through the region; it is found in every seed zone and in 19 of the 30 conservation areas (see conservation area maps in appendix 1). Because of this distribution and lack of tree harvest, much of the habitat is intact and provides a large base for gene conservation. However, this type of protection does not prevent habitat destruction and loss of genetic resources due to large fires, mountain pine beetle infestation, and blister rust infection and mortality and eventual losses caused by climate warming. Recently, large fires have destroyed large areas of habitat in conservation areas 202, 203, 204, 205, 502, 603, and 604.

There are ways to mitigate some of these losses. Individual trees that have proven to be rust resistant or otherwise genetically unique or critical for cone collection can be pruned of limbs with visible rust cankers to prolong their lives, and treated to limit attack by mountain pine beetles (see the Mountain Pine Beetle section, earlier in this document). These treatments are expensive and labor intensive, however, and at this time their use is very limited.

We can also ask fire managers to limit or prevent stand-replacing fires in areas specified for whitebark pine conservation. Under the Forest Service program of Wildland Fire Use (USDA Forest Service, N.d), we have the opportunity to incorporate strategies for managing wildfires that will best safeguard and improve whitebark pine habitat.

Additionally, as national forests in the Pacific Northwest complete forest land management plan revisions, specific recommendations for protecting or minimizing fire suppression-related damage to whitebark pine and fire rehabilitation can be included.

Ex Situ

Given that losses will continue, the implementation of an *ex situ* gene conservation plan is critical. The value of the various types of *ex situ* genetic resources will depend on

Wildland fire use is the management of naturally ignited fires to achieve resource benefits, where fire is a major component



of the ecosystem. Many natural resource values can be enhanced by allowing fire to play its natural role where private property and social values can be protected.

For centuries lightning caused fires have created vegetative diversity, such as a mixture of wildlife habitats, while



eliminating heavy fuel accumulation. Wildland fire use can be managed to burn in a natural way to provide benefits to the resources until fall rain or snow storms put it out. Wildland fires are a fact of western life—a natural component of the ecosystem in which we live.

www.fs.fed.us/fire/fireuse/wildland fire use/use index.html

how these collections are sampled and stored. The Pacific Northwest Region program will focus on seed, seed production areas, and clone banks. It also may be possible to store pollen samples if these can be collected when cones are caged in the spring.

The Forest Service is in the process of developing a national program for genetic conservation of forest tree species (Tkacz 2008). One of the primary *ex situ* gene conservation activities is to, "Make seed collections to sample the span of genetic variations present in the species." Following the seed sampling protocol, we developed a sampling plan for whitebark pine in the Pacific Northwest (table 9).

Collection areas were assigned to single conservations areas or combinations of conservation areas that experience minimal gene flow due to geographic isolation. Duplicate samples will be stored at the Forest Service Dorena Genetic Resource Center (Dorena) and at the National Center for Genetic Resources Preservation (NCGRP) under a memorandum of understanding (MOU) with the USDA Agricultural Research Service in Fort Collins,



Seed samples packed for long-term storage.

National Center for Genetic Resources Preservation

Color variation in seed collected from two whitebark pine trees.



Richard Sniezko, USFS



The vault area at the National Center for Genetic Resources Preservation.

Colorado. A minimum of 500 seeds per family are required under this MOU. Additionally, a minimum of 300 seeds per family should be stored at Dorena. Thus, we will aim for collections of 800 seeds from each of 25 trees per collection area. The seed stored at Dorena will be used for rust resistance screening, operational seedling production, and research. In some cases it will not be the number of seeds that will be difficult to reach, but the number of trees per seed zone. It will be challenging to accomplish these seed collection goals in smaller, isolated conservation areas. Completion of the collections will take considerable time and resources to accomplish, probably 8–10 years.

Over the past 7 years we have made considerable progress in making seed collections across the Pacific Northwest (table 9). This seed is stored at the Dorena as individual families and has been used in rust resistance testing. Some of this seed can be used to start long-term seed storage at NCGRP.

Blister Rust Resistance Testing

Genetic resistance to *Cronartium ribicola* is the key to maintaining viable populations of whitebark pine

| Table 9. Seed collection plan for ex situ gene conservation | | | | |
|---|-----------------|-------------------------------------|-------------------------------------|-------------------------------|
| Seed zone | Collection area | Conservation area | Number of trees per collection area | Number of trees per seed zone |
| 1 | 1 | 101 | 25 | 25 |
| 2E | 1 | 203, 204, and 205 combined | 25 | 75 |
| 2W | 1 | 206 and 207 combined | 25 | 25 |
| 3 | 3 | 301, 302, 303 | 25 | 75 |
| 4 | 1 | All areas combined | 25 | 25 |
| 5 | 3 | 501, 502, 503, and 504 combined 505 | 25 | 75 |
| 6 | 3 | 601, 602, and 603 combined 604 | 25 | 75 |
| 7 | 3 | 701, 703, 704 | 25 | 75 |
| 8 | 3 | 801, 802, 803 | 25 | 75 |

in the presence of this pathogen. C. ribicola is now a permanent resident of our forest ecosystems, and managing the naturally occurring genetic resistance offers a method of establishing a new equilibrium with this introduced pathogen that allows whitebark pine to survive and coexist with the pathogen. Few, if any, whitebark pine are likely to be "immune" to the disease; under suitable conditions, most whitebark pine trees will get cankers. However, varying degrees of resistance exist, including some that should be of immediate utility and others that will require breeding or placement into orchards to enhance their utility. Maintaining a diversity of resistances will likely be the best option for maintaining durability of resistance to C. ribicola. Unfortunately, the frequency of trees with high levels of natural resistance is generally very low in natural populations of whitebark pine.

Short-term screening assays can be used to evaluate progenies of hundreds or thousands of parent trees for resistance. This process will characterize each population as to the frequency and type of resistance. Once resistant parent trees are identified, they (or their resistant progeny) can be established in orchards, or seed can be collected from them in the forest, or breeding can take place to increase the level of resistance or combine resistances. Only with a long-term concerted effort will it be possible to achieve the goal of having populations of whitebark pine that are genetically resistant to *C. ribicola* while

maintaining high levels of genetic variation and good adaptability.

The Dorena Genetic Resource Center (Dorena), a component of the regional genetics program of Pacific Northwest Region (and a partner with the regional Forest Health Protection group), has established protocols for blister rust resistance testing of whitebark pine. These protocols are based on those developed and successfully used for screening of western white pine (*P. monticola*) and sugar pine (*P. lambertiana*) over the past 5 decades (Danchok et al. 2003).

Resistance testing involves inoculation of young (usually 2-year-old) seedlings with spores of *C. ribicola* and evaluation of seedlings for up to 5 years



Preparing for blister rust inoculation in inoculation chamber at Dorena.

Richard Sniezko, USFS

after inoculation. Inoculation usually takes place in late August or during September (which coincides with time of natural infection in the field). Seedlings are moved into a climate-controlled inoculation chamber. Temperature within the inoculation chamber is maintained at around 16.7° C (62° F) and relative humidity at 100 percent. Ribes spp. are the alternative host for C. ribicola, and spores from infected Ribes spp. are necessary to infect the pines. *Ribes* spp. leaves infected with C. ribicola at the telial stage are collected from forests in Oregon and Washington or from the *Ribes* garden at Dorena. The *Ribes* leaves are placed on wire frames above the seedlings, telial side down. Spore fall is monitored until the desired (target) inoculum density of basiospores is reached for each box; the Ribes leaves are then removed. After the target inoculum density is reached for the last box, the temperature is raised to 20° C, and the seedlings are left in the inoculation chamber for approximately 48 hours to ensure spore germination and infection of the pine needles. See http://www.fs.fed.us/r6/dorena/ photos/rust/ for photos of the inoculation process and other aspects of blister rust resistance testing.

Following inoculation, the seedlings are transported outside. The seedlings are evaluated over a period of 5 years for the presence of disease symptoms and mortality. The first symptoms to develop are needle lesions, or 'spots.' These are typically assessed approximately 9 months and 1 year after inoculation. Presence and number of stem symptoms along with mortality is assessed annually for 5 years after inoculation.

Since the underlying basis and the inheritance of many of these mechanisms is unknown, and there may be geographic differences in the types of resistance mechanisms, the Region 6 rust resistance screening program currently focuses on broad resistance categories (see Kegley and Sniezko 2004, Sniezko 2006, Sniezko et al. 2007 for some details on white pine resistance work). Those categories include the following:

- 1. Preventing stem infection (canker-free);
- 2. Reduced number of infections (stem infections or needle lesions);



Blister rust infection (needle lesions or 'spots') on primary needle of young whitebark pine seedling, approximately two months after inoculation.

- 3. Latent infections—stem symptoms occur 1 or 2 years later than for susceptible trees;
- 4. Stem infection occurs, but tree survives and is relatively vigorous; stem symptoms may be active (tolerance and slow canker growth) or inactive (bark reaction or inactive canker);
- 5. Stem infection occurs and tree dies, but the blister rust fungus is slowed, and mortality occurs at a later time period than for most trees (slow canker growth or partial bark reaction).

One or more of these resistances may be present in a seedling family. The frequency of resistant seedlings coming from each parent tree will depend on the inheritance of the resistance traits and the frequency of resistance in the pollen parents pollinating each tree.

Seedlings from more than 150 seed lots collected prior to 2004 from individual parent trees from national forests (Oregon and Washington), national parks (Oregon and Washington), and on Confederated Tribes of Warm Springs lands have been inoculated with *C. ribicola* to evaluate them for genetic resistance. More than 200 additional families from more recent seed collections will be inoculated in September 2008. (See table 1 in Sniezko et al. 2007 for a listing of numbers of parent trees from each geographic area whose progenies are under test at Dorena).

The first trial has been assessed for three years so far. The inoculation procedures at Dorena have been successful in producing needle infection on approximately 100 percent of the trees. Detailed

preliminary early results from the first trial are summarized elsewhere (Sniezko et al. 2007). Updated results from both the first and second trials indicate that genetic resistance to white pine blister rust is present in whitebark pine in Oregon and Washington.

In the first trial of 43 families, at 3 years after inoculation, some families show 30–40 percent or higher survival compared to less than 5 percent for many other families. Seedlings in these higher surviving families show one or more of several traits: canker-free, latent cankers, or ability to live longer with cankers. All three of these traits are generally present in some of the seedlings in the top surviving families. In this trial and a more recent larger one, there appears to be a trend of increasing resistance as one goes from southern Cascade populations (for example, Crater Lake National Park) to northern Cascade populations (for example, Mt. Rainier National Park). The populations in eastern Oregon tested so far also have low levels of resistance overall, but progeny of a few parents show moderate levels of resistance.

In the second trial (94 families), 2 years after inoculation, progeny of some parent trees have moderate to high levels of resistance (for example, more than 50 percent of seedlings are canker-free compared to other families with 90–100 percent of seedlings cankered). This trial will be assessed for 3 additional years to screen for latent infections and any other resistance responses that might vary between families.



Dramatic contrast of blister rust resistant and non-resistant seedling families of whitebark pine 2½ years after artificial inoculation.

The frequency of parent trees with resistance varies by population, and some populations will need several times the number of selections to obtain a designated number of resistant offspring. There are several types of resistance ranging from canker-free ("complete" resistance) to seedlings that live for several years or more with cankers or seedlings that show cankers one or more years after other seedlings. Each of these first two trials will be followed for several additional years to more closely delineate the types of resistance present.

Results of this early work indicate that it should be possible to use resistance testing of seedling progenies to confirm resistance of the candidate parent trees. The Dorena facility has the capacity to test hundreds of seedling families at once (perhaps 600 or more), provided budgets permit. Thus, the main constraint for identifying enough resistant parent trees for restoration within each breeding zone may be location of additional field selections by field personnel and collection of sufficient seed for testing.

The parent trees in the field can be monitored as defacto permanent plots to gauge the actual field resistance and durability of this resistance. In addition, early plantings of resistant materials should be monitored to confirm resistance under actual field conditions, as well as to note any possible change in the virulence of the rust population.

Seed Collection and Tree Selection

Seed is the foundation of our whitebark pine restoration program. Seed is needed for planting, rust resistance testing, and gene conservation. Collecting whitebark pine seed is very challenging and expensive (Ward et al. 2006a). Cones must be caged to protect them from harvest by Clark's Nutcrackers. A variety of collection methods may be used including climbing, ladders, and a tree-tong (Davies and Murray 2007, Murray 2007). Each tree must be visited twice—once to cage, later to collect. Many whitebark stands are remote and require travel by foot over long distances and overnight trips. The number of Forest Service certified climbers as well as contractors with professional climbers are limited.



Seeds in whitebark pine visible after cone scales have been removed.

Don Pigott, USFS



Cone collection by climbing.





Cone collection by lift.

More than 350 whitebark pine trees have been selected (table 8, earlier) following guidelines that are provided in Shoal (2008). Trees are primarily selected when cone crops are present. The number of trees selected in each conservation area is the result of variation in accessibility to cone bearing trees by roads and trails, cone productivity, and seed need.

It would be ideal to have between 15 and 30 rustresistant trees for each seed zone. These could be combined into seed zone-wide mixes. Early test results found that the number of families found to be resistant varied from 0 percent to 95 percent by conservation area. Assuming that on average 1 in 5 trees will be resistant, seed from 75 to 150 candidate trees in each seed zone must be collected in order to find 15 to 30 rust-resistant families. This will not be possible in all zones because of the small size of the habitat, poor road access, and the cost of seed collection. Undoubtedly, there will be different approaches to seed production and use across the region based on level of resistance, seed availability, and need. When tests of more than 200 families are completed in 2013, the results will provide an opportunity to design the most appropriate program for each seed zone.

Seed Production

One method that will be used to produce genetically resistant seed for planting or sowing projects is to establish seed production areas. Seedlings from 15 to 30 rust-resistant families will be planted in an area of whitebark pine habitat that is easily accessible by road. Seed production areas are less expensive to establish and maintain than seed orchards. Because there is no plan to breed trees for future generations in a seed production area, fewer families are planted on a smaller number of acres and the identity of the individual families is not maintained. This is important given the lack of suitable terrain and limited financial resources. Seed from these trees will be combined into a single seed lot and used to produce seed and seedlings for planting. It will be 7–10 years before the results of resistance testing will provide us with enough families to plant any seed production areas.

It is premature to decide now if whitebark pine seed orchards are a viable option for the Pacific Northwest Region. Several pilot projects are underway that can help answer questions such the best timing for scion collection and grafting, and whether grafted trees can survive at low elevations where orchards would be easier to manage. The option to develop seed orchards will be assessed when this restoration strategy is updated in 2014.

RESEARCH, INVENTORY, AND MONITORING OPPORTUNITIES

There is much that we don't know about whitebark pine and how best to approach the factors that threaten it. We also have very little practical experience with planting the species in the wild or with other kinds of whitebark pine silvicultural treatments in the Pacific Northwest. We do know more about western white and sugar pines, and that knowledge will perhaps provide

some guidance. Still, for specific information about whitebark pine, we must learn as we go.

It is clear that to foster learning, monitoring must be an integral part of all whitebark pine restoration projects. If they are not monitored well enough to learn from them, projects will have greatly diminished value. The cost of monitoring should be included in each project's budget.

Planting trees from phenotypically resistant parent trees will likely be the main thrust of the next 5 years of restoration projects. Project areas and perhaps individual trees should be located using global positioning system devices; photo points should be established where appropriate; and periodic measurements and observations should be made and recorded. For planted trees, data are needed on survival, growth, condition over time, causes of damage, and influence of site and micro-site. Efforts to maintain and protect the phenotypically resistant parent trees also should be monitored.



Monitoring the condition of a whitebark pine stand.

As part of the overall whitebark pine restoration strategy, a vehicle for gathering, collating, analyzing, and disseminating monitoring results from restoration projects is needed. Creation of a whitebark pine restoration strategy coordinator position in the region to lead this kind of effort could prove effective.

With the substantial number of surveys on whitebark pine condition that have been done in Washington and Oregon (Shoal and Aubry 2006, Ward et al. 2006b), a good baseline exists for keeping track of the vigor and reproductive success of the species in the future through periodic re-measurements of the same stands. More demographic information might be gathered at the same time. The efforts to map suitable whitebark pine habitat that were associated with preparation of this strategy have also provided information on areas where whitebark pine populations may exist but where their status is currently unknown. These areas should be evaluated in the future.

Interest in whitebark pine among academic and agency scientists is great. Valuable research has been done, and future research projects that will fill data gaps, especially those that apply to management-related issues, will be extremely useful. Providing funding may not be easy but research on whitebark pine should be encouraged and supported to whatever degree possible. Also collecting enough whitebark pine seed to make an adequate amount available for research projects should be a priority.

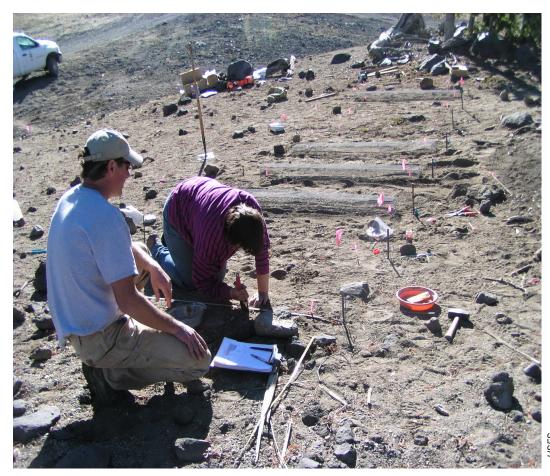
As part of the whitebark pine restoration strategy, a concerted effort to identify and prioritize research needs would be worthwhile and could be organized in an ad hoc fashion or by a whitebark pine restoration strategy coordinator. A myriad of important research questions could be addressed, such as:

- What roles do *Pedicularis* and *Castellija* species play in the life cycle of *C. ribicola* in Pacific Northwest whitebark pine sites?
- How does the timing of stages in the life cycle of *C. ribicola* in high-elevation sites influence infection of whitebark pine, and how important is spore production in lower elevation ecosystems in the Pacific Northwest?

- Are there genetic markers available or that can be developed to assist in early selection for white pine blister rust resistance?
- What are the effects of cone and seed insects on whitebark pine seed production in natural stands and seed orchards?
- What is the influence of climate change on the life cycles of *C. ribicola*, seed and cone insects, and mountain pine beetle in the Pacific Northwest?
- How might climate change influence frequency and intensity of wildfires in Pacific Northwest whitebark pine stands?
- How has climate change already affected whitebark pine habitat?
- What has been the role of fire in the past in whitebark pine habitat?
- How are fuel management dynamics best managed in different parts of whitebark pine's habitat?
- How often and where would prescribed fire benefit different parts of whitebark pine's habitat and what would be the effects on mountain pine beetle activity?
- Do whitebark pine seedlings survive and grow better when they occur in a close group (as is often the case in nature when they are planted by nutcrackers) than when they occur as widely spaced individuals?
- What are the influences of various kinds of microsites on success of whitebark pine planting?
- What type of site preparation is necessary and best for successful planting of whitebark pines?
- What is the best type of stock for planting (bareroot or container)?
- What treatment regimes are best for stimulating whitebark pines to produce cones?
- What timing is best for successful whitebark pine planting?
- Is it possible to successfully direct-sow whitebark pine seeds in the field?
- Could pruning be a useful tool in managing white pine blister rust in whitebark pine stands?

- How can thinning of trees be incorporated with other techniques such as prescribed fire to maintain whitebark pine habitat and deter mountain pine beetle attack?
- How would thinning affect mountain pine beetle activity in different stand and landscape conditions?
- Are there already areas, especially in whitebark pine's lower elevation habitat, where restoration attempts are likely to be fruitless?
- Are there currently areas higher in elevation than the obvious whitebark pine habitat where restoration activities should be directed for potential future habitat?

- What information is needed to make meaningful dynamic models of whitebark pine habitat in a changing climate scenario, including models that could provide site-specific information to managers for determining the best places to undertake restoration efforts?
- Are there indicator species that can be used to predict
 where it is no longer wise to attempt restoration or
 places where restoration should be attempted? Are
 there shrub and herb species that respond more
 rapidly to climate change than whitebark pine that
 could be used in such an endeavor?



Planting whitebark pine seeds in a planting feasibility research project.

ADAPTIVE MANAGEMENT

An adaptive management approach is highly appropriate for whitebark pine restoration in the Pacific Northwest. Given our lack of past experience with whitebark pine planting and silviculture and the urgency of doing some kind of mitigation as quickly as possible in stands that are obviously suffering significant amounts of mortality and decline, adaptive management is the only realistic way to proceed. We must try things, monitor results, and learn from successes and failures.

This restoration strategy is intended to cover the next 5 years. At the end of that time, new information applicable to whitebark pine restoration and conservation should be used to prepare a refined strategy. Adjustments in approach may be needed even sooner if based on compelling evidence. Much significant information will be generated by results of on-the-ground projects. Although the emphasis for the next 5 years will be on planting pertinent areas with whitebark pine seedlings, it is to be hoped that significant new information will be gained regarding principles of propagating, handling, and planting the species as well as differences in survival and growth associated with different sites and micro-sites and different levels of vegetative competition within the region.

New information should be gathered in one place and ultimately evaluated. This could be the responsibility of a regional whitebark pine restoration coordinator, as suggested in the previous section. Such a position could also handle dissemination of results to managers in the field, as well as training and education programs.

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GLOSSARY

- acclimation—response by an organism that enables it to tolerate a change in a single factor (eg temperature) in its environment. Also, phenotypic adaptation to environmental fluctuations; the gradual and reversible adjustment of physiology or morphology as a result of changing environmental conditions.
- adaptation—In the evolutionary sense, some heritable feature of an individual's phenotype that improves its chances of survival and reproduction in the existing environment
- **adaxial**—Situated on the same side as or facing the axis.
- **aeciospore**—A non-repeating, asexual spore borne in an aecium; the spore type of *C. ribicola* that is produced on a five-needle pine and spreads to and causes infection on an alternate host
- allele—A shorthand form of allelomorph, one of a series of possible alternative forms of a given gene differing in DNA sequence, and affecting the function of a single product (RNA and/or protein). If more than two alleles have been identified in a population, the locus is said to show multiple allelism.
- **allozymes**—Allelic forms of an enzyme that can be distinguished by electrophoresis, as opposed to the more general term isozyme.
- alternate host—A second host required for completion of the life cycle of a rust fungus; in the case of *C. ribicola*, for example, *Ribes*, *Pedicularis*, or *Castellija* species are alternate hosts and five-needle pines are considered to be primary hosts.
- **anthropogenic**—Of, relating to, or involving the impact of humans on nature.
- **basidiospore**—A sexual spore produced on a basidium where fusion of compatible nuclei and reduction division occurs; the spore type of *C. ribicola* that spreads from an alternate host and initiates infection on a five-needle pine.
- cache—In relation to seed dispersal by animals, refers to a discrete site selected by an animal for temporary cone or seed storage. Caches may contain one or many cones or seeds depending on the species of animal storing and the species plant being stored; also the act of placing, hiding, or storing provisions in such a place.
- **canker**—An area of necrosis on a stem or branch, usually with a sunken surface.

- **chloroplast**—The chlorophyll-containing photosynthesizing organelle of a plant.
- **cold hardiness**—A measurement of a plant's response to declining temperatures including acclimation, midwinter hardiness, and deacclimation.
- common garden—A scientific study in which many families of a given plant species sampled from an identified geographic area are grown in a common environment. Common garden studies generally include replications in two or more growing environments. Environmentally induced phenotypic differences between the plants are minimized, allowing observation and comparison of genetically adapted traits. Common garden studies are used to determine seed transfer zones.
- connivent—Converging but not fused.
- electrophoresis—The movement of the charged molecules in solution in an electrical field. The solution is generally held in a porous support medium such as filter paper; cellulose acetate (rayon); or a gel made of starch, agar, or polyacrylamide. Electrophoresis is generally used to separate molecules from a mixture, based upon differences in net electrical charge and also by size or geometry of the molecules, dependent upon the characteristics of the gel matrix.
- **embryo**—The young plant within a seed, usually comprised of the plumule, radicle, and cotyledons.
- **epigeal germination**—Growing above the surface of the ground, the cotyledon forced above ground by elongation of the hypocotyl.
- **etiology**—The causes of a disease or abnormal condition; a branch of knowledge dealing with causes.
- **fascicle**—A bundle or cluster of stems, flowers, or leaves, such as the bundles in which pine needles grow.
- **fitness**—The relative ability of an organism to survive and transmit its genes to the next generation.
- **five-needle pine**—A pine in the subgenus *Strobus*, also known as a soft or white pine; characterized by having five needles per fascicle.
- **fundamental niche**—The total range of environmental conditions that are suitable for a species' existence, without taking into account the effects of interspecific competition and predation from other species.
- **gamete**—A mature germ cell possessing a haploid chromosome set and capable of initiating formation of a new individual by fusion with another gamete.

- **granivore**—An animal that selectively eats seeds.
- **gene flow**—The exchange of genes among different populations of the same species produced by migrants, and commonly resulting in simultaneous changes in the gene frequencies at many loci in the recipient gene pool.
- **genetic differentiation**—The accumulation of differences in allelic frequencies between isolated or semi-isolated populations due to various evolutionary forces such as selection, genetic drift, gene flow, assortative mating, etc.
- **genetic drift**—The random fluctuations of gene frequencies due to sampling errors. While drift occurs in all populations, its effects are most evident in very small populations.
- **girdle**—To kill a plant by interrupting the flow of water and nutrients around the stem.
- **heterozygosity**—The conditions of having one or more pairs of dissimilar alleles.
- **homozygosity**—Having identical rather than different alleles in the corresponding loci of homologous chromosomes and therefore breeding true.
- **hybridize**—To cause the production of hybrids, to interbreed; a hybrid is an offspring of two animals or plants of different species.
- **inbreeding depression**—Decreased vigor in terms of growth, survival, or fertility following one or more generations of inbreeding.
- **infection**—The establishment of a pathogen in its host after invasion.
- **infestation**—Living on or in as a parasite; used to signify successful colonization of a tree by bark beetles.
- intolerant—Not adapted to enduring a specific condition; in the case of trees, usually used to describe a species that is intolerant of shade and does not grow well in situations where it is shaded by other trees.
- **keystone species**—A species whose effect in an ecosystem is disproportionately large relative to its abundance; the term has also been widely used to denote a species on which associated species depend for support.
- **krummholz**—A shrub-like or prostrate form of a highelevation tree that has developed its low, bent shape because of frequent exposure to high winds.

- **larder-hoard**—Method of food storage by animals in which items are concentrated in one or few caches. Larders are visited multiple times.
- **maladaptation**—Incomplete, inadequate, or faulty adaptation.
- markers—A gene with a known location on a chromosome and a clear-cut phenotype, used as a point of reference when mapping a mutant.
- **megagametophyte**—The eight-celled embryo sac that develops within the ovule of an angiosperm.
- **microsatellite**—Tandemly repeated DNA sequences of one to six bases.
- microsite—A small site with its own climatic conditions that may differ from those in its surroundings; for example, a damp, low-lying site in an otherwise dry area.
- midden—An accumulation of cone debris that collects beneath the preferred feeding perches of squirrels. Squirrels may use middens for food storage.
- **monoecious**—Producing pistillate and staminate flowers on the same plant.
- **monoterpenes**—a specific class of terpenes, which are hydrocarbons, and are the primary constituents of essential oils in plants and a major component of conifer resin.
- **mutate**—To undergo a fundamental change in heredity, producing new individuals that are basically unlike the parents.
- **mutation**—The process by which a gene undergoes a structural change; a modified gene resulting from mutation; by extension, the individual manifesting the mutation.
- mutualism—An interaction between two or more species where both species derive benefit. Mutualisms can be lifelong interactions involving close physical and biochemical contact (known as symbiosis) such as those between plants and mycorrhizal fungi; they can also be briefer, non-symbiotic interactions, such as those between flowering plants and pollinators or seed dispersers. Mutualisms may be optional (facultative) or obligatory.
- **mycelium**—The mass of filamentous fungal strands (hyphae) that forms the vegetative portion of a fungus.
- ovoid—Shaped like an egg.

- pathogen—A disease-causing agent.
- **phenology**—The study of periodic biological phenomena, such as flowering, breeding, and migration, in relation to climatic conditions.
- **phenotypically resistant**—Having the appearance of being resistant; for example, a tree that appears to be healthier than its neighbors when all have had equal exposure to a pathogen such as *C. ribicola*.
- **polymorphic locus**—A genetic locus, in a population, at which the most common allele has a frequency less than 0.95.
- **population**—A local (geographically defined) group of conspecific organisms sharing a common gene pool; also called a deme.
- **pruning**—Cutting branches off a tree's stem for a specific purpose.
- **pycniospore**—A rust fungus spore type that is borne in a pycnium and serves as a gamete; in the case of *C. ribicola*, pycniospores are produced on the five-needle pine host and do not induce additional infections.
- **realized niche**—The part of the fundamental niche that a species actually occupies.
- **refugia**—Areas where special environmental circumstances have enabled a species or a community of species to survive after extinction in surrounding areas.
- **resistance**—The ability of an organism to overcome completely or to some degree the effect of a pathogen or other damaging factor.
- **restoration**—To bring back or put back into a former or original state; management aimed at reversing the decline of a species and returning it more nearly to a former desirable condition.
- scatter-hoarding—A method of food storage by animals in which items are cached in many locations throughout an individual's home range. Unlike larders, scatter-hoards are usually visited only once for caching and once for retrieval.
- selection—The process of determining the relative share allotted individuals of different genotypes in the propagation of a population. The selective effect of a gene can be defined by the probability that carriers of the gene will reproduce.

- **selfing**—Undergoing self-pollination or self-fertilization.
- **sessile**—Attached directly by the base and not raised upon a stock or peduncle.
- **source-sink**—A population structure where one population, the source, is permanent and supplies individuals to restart one or more transient populations (sinks).
- **spore**—A minute propagule that functions in the manner of a seed but lacks an embryo.
- **stomates (stomata)**—The minute pores in the epidermis of a needle, leaf, or stem through which gases and water vapor pass.
- **strobilus (plural strobili)**—the fruiting body of a gymnosperm.
- stratification—A pre-germination treatment intended to break dormancy in seeds that is accomplished by exposing them for specific times to moisture in cold and warm conditions.
- **sublingual pouch**—A diverticulum or sack-like extension of the floor of the mouth under the tongue used by birds in the genus *Nucifraga* to carry seeds.
- **teliospore**—The spore type of a rust fungus in which male and female nuclei fuse and from which the basidium arises. In the case of *C. ribicola*, teliospores are formed on telial colums on the leaves of alternate hosts.
- **trait**—Any detectable phenotypic property an organism; synonymous with phenotype, character.
- **urediniospore**—An asexual dikaryotic rust spore produced in an uredinium. In the case of *C. ribicola*, uredinia and urediniospores are produced on the leaves of alternate hosts and urediniospores re-infect alternate host leaves contributing to build-up of inoculum.
- variation—Divergence among individuals of a group, specifically a difference of an individual from others of the same species that cannot be ascribed to a difference in age, sex, or position in the life cycle. The variations of evolutionary significance are gene-controlled phenotypic differences of adaptive significance.
- **virulent**—Highly infective; marked by a rapid, severe, and malignant course.

Acronyms

| ACRONYM | FULL MEANING |
|---------|--------------------------------------|
| ABAM | Abies amabalis (Pacific silver fir) |
| ABLA | Abies lasiocarpa (subalpine fir) |
| CA | conservation area |
| DBH | diameter at breast height |
| GIS | geographic information system |
| Hwy | highway |
| LALY | Larix Iyallii (subalpine larch) |
| MPB | mountain pine beetle |
| MBS | Mt Baker-Snoqualmie National Forest |
| Mt | Mountain |
| NEPA | National Environmental Policy Act |
| NPS | National Park Service |
| OCRA | Oregon Cascades Recreational Area |
| PAG | Plant association group |
| PIAL | Pinus albicalis (whitebark pine) |
| PICO | Pinus contorta (lodgepole pine) |
| PIEN | Pinus engelmannii (Engelmann spruce) |
| PIMO | Pinus monticola (Western whitepine) |
| PSME | Pseudotsuga menziesii (Douglas-fir) |
| TSME | Tsuga mertensiana (mountain hemlock) |
| WPEF | Whitebark Pine Ecosystem Foundation |