

THE RAPID DECLINE OF WHITEBARK PINE COMMUNITIES: ECOLOGICAL AND BIODIVERSITY IMPLICATIONS

Diana F. Tomback¹
Department of Biology
University of Colorado at Denver
P.O. Box 173364
Denver, CO 80217, USA

Sabbatical leave address:
USGS Science Center
Glacier National Park
West Glacier, MT 59936

Abstract: White pine forest communities of the western United States are disappearing rapidly from the landscape as the result of widespread infection from the exotic fungal pathogen, white pine blister rust (*Cronartium ribicola*), and nearly a century of fire exclusion. Fire exclusion limits opportunities for regeneration, resulting in successional replacement of white pines by shade-tolerant conifers. White pine blister rust, a fatal disease that infects five-needled white pines, initially eliminates seed cone production by killing branches, and eventually girdles and kills the tree. To date, white pine blister rust has infected six pines: western white (*Pinus monticola*), sugar (*Pinus lambertiana*), whitebark (*Pinus albicaulis*), limber (*Pinus flexilis*), southwestern white (*Pinus strobiformis*), and foxtail (*Pinus balfouriana*). Susceptible but not yet infected are the two bristlecone pines, the Great Basin (*Pinus longaeva*) and Rocky Mountain (*Pinus aristata*). As these white pine forest types decline, so will the ecosystem services they provide and the tremendous biodiversity they represent collectively. Whitebark pine in particular has suffered precipitous losses, and the consequences of these losses to wildlife and ecological processes are discussed in detail.

Introduction

More than half a century ago, the conservationist Aldo Leopold (1949) wrote, "The white-pine blister rust, stopped in its westward march by the treeless plains, effected a new landing via the back door, and is now romping down the Rockies from Idaho toward California." This quote refers to the inadvertent, independent introductions of the exotic fungal pathogen, white pine blister rust (*Cronartium ribicola*) to both eastern and western North America in the 1890's and 1910, respectively, and the dire consequences for North American five-needled white pines (Family Pinaceae, genus *Pinus*, subgenus *Strobus*) (Hoff and Hagle 1990, McDonald and Hoff 2001). In this paper, I describe how blister rust together with decades of fire suppression is impacting western montane and subalpine zone landscapes and their biodiversity, using whitebark pine (*Pinus albicaulis*) as a particularly important case history.

Blister rust: life cycle and western distribution

White pine blister rust, native to Asia, requires five-needled white pines and shrubs of the genus *Ribes*, the gooseberries and currants, as alternate hosts (McDonald and Hoff 2001). The complex life cycle of blister rust involves five different spore types, several with restrictive requirements of cool temperatures and high humidity for spore production or transmission. Aeciospores, which are produced by blister rust cankers in living bark tissue of white pines, transmit the disease to *Ribes* in late spring when the shrubs leaf out; these spores live for weeks and may be blown by wind over distances as great as 500 km (Mielke 1943). Urediniospores are produced throughout the summer, spreading blister rust over short distances from shrub to shrub. In late summer, basidiospores are produced by *Ribes*, transmitting the fungus relatively short distances to pines and thus completing the cycle. Basidiospores infect pines by entering through the needle stomata, and mycelia grow through the vascular tissue of the needle into the stem or

branch of the tree. Usually after two years the branch or stem at the site of infection becomes a swollen canker that may produce aeciospores annually, until it is girdled by the rust and dies. Although branch cankers may eventually grow down into the stem and kill the entire tree, branches usually die first, resulting in loss of seed production.

The frequent occurrence of favorable conditions for spore production and transmission enabled blister rust to spread rapidly from its western point of introduction in 1910 near Vancouver, British Columbia, throughout the Pacific Northwest and Intermountain West of both the United States and Canada (Kendall and Keane 2001, McDonald and Hoff 2001). Various countermeasures were pursued, including *Ribes* eradication programs and the use of fungicides, but these came after the initial spread and provided little control (McDonald and Hoff 2001). As illustrated by McDonald and Hoff (Fig. 10-2, 2001), as of 1925 the rust was found as far south as southern Washington and as far east as eastern Idaho. By 1953, it had traveled down the Cascades and Sierra to central California and east through western Montana and the Greater Yellowstone. By 1966, it was detected in the southern Sierra Nevada and had spread east through Wyoming. By 1998, blister rust had been detected in the Black Hills of South Dakota and in northern Colorado, and for the first time in southwestern white pine in southern New Mexico.

Today, blister rust infects six five-needled white pines of the West: The disease has infected and killed trees throughout all or much of the range of western white pine (*Pinus monticola*), sugar pine (*Pinus lambertiana*), whitebark pine (*Pinus albicaulis*), and limber pine (*Pinus flexilis*), and in part of the range of southwestern white pine (*Pinus strobiformis*), and foxtail pine (*Pinus balfouriana*). The two bristlecone pines, Great Basin (*Pinus longaeva*) and Rocky Mountain (*Pinus aristata*), are not yet infected but considered susceptible (Hoff et al.

1980); extreme vigilance is necessary to protect the ancient bristlecone pines of the White Mountains in eastern California. Where blister rust occurs, the infection incidence per stand (percent trees infected) and per tree (number of cankers per tree) are variable (e.g., Smith and Hoffman 2000), the likely consequence of regional wind patterns, local climate, and the local density, species, and distribution of *Ribes* (McDonald and Hoff 2001). Over time, however, the trend appears to be an intensification of infection within a stand.

A century of fire suppression: compounding the losses

In 1910, the same year that blister rust came to the West, the northern Rocky Mountains experienced “the Big Blowup”—the most devastating fire event in the 20th century. Three million acres burned, most within a two-day period, killing 85 people and destroying several small towns (Arno and Allison-Bunnell 2002). This event led to the birth of a national fire exclusion policy, which doubled the jeopardy for five-needled white pines.

The five-needled white pines of the West are all moderately to highly dependent on fire and other disturbances for establishment on favorable sites. In the absence of fire, they are successional replaced by more shade tolerant species (e.g., Rebertus et al. 1991, Neuenschwander et al. 1999, Arno 2001). Foxtail, bristlecone, whitebark, and limber pine form self-replacing climax communities at or above timberline or on droughty, windy sites; but fires in these communities also favor establishment of these white pines. As the historical fire interval is lengthened by fire suppression, white pines in successional communities senesce or are out-competed, with dwindling presence over time. Clearly, the combination of blister rust and fire exclusion results in rapid declines. In areas with high blister rust incidence, crown kill, and mortality, even if fire does occur, seeds are virtually unavailable and little regeneration is possible.

These effects are well illustrated by the loss of western white pine from the Inland Northwest, where the historical fire return interval was about 200 years. Once touted as the "King Pine" and the center of a vigorous logging industry, the combination of logging, fire suppression, blister rust, and mountain pine beetle (*Dendroctonus ponderosae*) epidemics has reduced the pine to 5% of its former abundance (Neuenschwander et al. 1999). Western white pine communities have been replaced by shade-tolerant forests of grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*).

The ecology and biodiversity of whitebark pine communities

None of the five-needled white pines are likely to go extinct in the long-term, but their community types and ecological influences on the landscape are or will be greatly diminished. And, of all western five-needled white pines, none illustrates the impact of the decline as clearly as whitebark pine. The decline in the commercially valuable western white pine and sugar pine captured attention in the 1920's, prompting efforts to produce blister rust resistant planting stock by the 1940's and 50's (McDonald and Hoff 2001), but the spread of blister rust and increasing losses in whitebark pine went virtually unnoticed until the 1980's (Arno 1986, Kendall and Arno 1990). In fact, most of what we know about whitebark pine ecology and biology comes from studies over the last 25 years. Whitebark pine has a number of special attributes, even among the five-needled white pines that make its loss particularly significant. In particular, it plays an important ecological role as a wildlife food source, as a hardy early successional species, and as stress-tolerant, high elevation conifer.

Classification and distribution

Whitebark pine is of particular interest from an evolutionary and ecological perspective. It is the only North American member of the "stone pines," five white pines comprising

subsection *Cembrae* (subgenus *Strobus*, family Pinaceae), a group characterized by large, wingless seeds and “indehiscent cones,” that is, cones that do not open when seeds are ripe (Price et al. 1998). For seed dispersal, the five stone pines rely primarily on the “nutcrackers” (genus *Nucifraga*), birds that harvest pine seeds from cones and bury them in shallow caches in the ground for winter and spring food (Tomback and Linhart 1990). Whitebark pine seeds are dispersed by Clark’s nutcracker (*N. columbiana*) (Tomback 1978, 1982; Hutchins and Lanner 1982), which ranges throughout the higher mountains of the western United States and Canada (Tomback 1998). The nutcrackers are well adapted for this coevolved, mutualistic interaction: They have a long, sharp bill that enables them to open cones and remove seeds, an expandable throat pouch for carrying quantities of seeds, and a remarkable spatial memory for relocating seed caches (Tomback 1998 and references therein). They also readily cache seeds in newly burned areas or other open sites (Tomback 1986, Tomback et al. 2001a). Excess or forgotten seed caches germinate as snow melts or after summer rains, resulting in regeneration (e.g., Tomback 1982, Vander Wall and Hutchins 1983). Patterns of seed dispersal by nutcrackers, and the distances they fly to caching areas, shape the local and regional distribution of whitebark pine and other stone pines, as well as population genetic structure at multiple scales (e.g., Rogers et al. 1999, Feldman et al. 1999, Richardson et al. 2002; see Bruederle et al. 2001 and Tomback 2001 for overviews). Clark’s nutcrackers harvest and cache the seeds of other western pines with large, wingless seeds, including limber and southwestern white pine and the pinyon pines (*Pinus monophylla*, *Pinus edulis*), and ponderosa (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*).

Whitebark pine ranges from the northern coastal mountains of central British Columbia south through the crest of the Cascade Range and Sierra Nevada to south-central California, and

from the Canadian Rocky Mountains south through the Rocky Mountains of Idaho, Montana, and southwestern Wyoming. Its distribution, although discontinuous, extends from 37 to 55° north in latitude and from 107 to 128° west in longitude (McCaughey and Schmidt 1990, McCaughey and Schmidt 2001, Ogilvie 1990). Extremely hardy, whitebark pine is a slow-growing conifer that tolerates harsh, high elevation environments, including steep slopes, windy exposures, poor soils, and the rigors of tree-line exposures (Arno and Hoff 1990, Weaver 2001).

In its center of abundance, the northern Rocky Mountains of the United States and the southern Rocky Mountains of Canada, whitebark pine occurs in successional communities in the upper subalpine zone, eventually replaced by shade-tolerant conifers in the absence of disturbance, such as fire. Mean fire return intervals in successional whitebark pine communities vary with fire intensity and geographic location, historically ranging from 30 to 400 years (Arno 2001 and references therein). Whitebark pine also occurs as climax and krummholz (dwarf tree island) communities on exposed sites and above timber-line, respectively (Arno and Hoff 1990, Arno 2001). Historically, whitebark pine communities accounted for 10 to 15 percent of forest cover in these geographic regions, with about half successional (Arno 1986, Arno 2001). In the more arid parts of its range, such as the Sierra Nevada, whitebark pine occurs as a climax species that is self-replacing over time and more limited in distribution (Tomback 1986, Barbour 1988).

Whitebark pine and biodiversity

Because whitebark pine performs several different ecological functions that enhance plant and animal diversity, it has been viewed as a "keystone species" (Tomback et al. 2001b). To begin, whitebark pine plays a major role as a wildlife food source in late summer and fall in years when cones are produced. The large, nutritious seeds are sought by nutcrackers, and a community of other seed-eating birds and small mammals, including woodpeckers, jays, ravens,

chickadees, nuthatches, finches, chipmunks, pine squirrels, ground squirrels, and mice (Tomback 1978, Hutchins and Lanner 1982, Lanner and Gilbert 1994, Tomback and Kendall 2001).

Whitebark pine communities also provide shelter, forage, nest holes, and burrows for a variety of other animals, including deer, elk, grouse, birds of prey, martens, coyotes, and a great diversity of small vertebrates and arthropods, many yet undescribed (Tomback and Kendall 2001).

Whitebark pine seeds comprise an important food for grizzly (*Ursus arctos*) and black bears (*Ursus americanus*), particularly before hibernation, in the Greater Yellowstone Area, the East Front of the Rocky Mountains, and the Greater Bob Marshall Ecosystem (Kendall 1983, Mattson et al. 2001). In fact, whitebark pine seeds and ungulates are considered the two most important grizzly bear foods in the Greater Yellowstone Area (Mattson et al. 1992). Bears obtain seeds by raiding the cone middens of red squirrels (*Tamiasciurus hudsonicus*) (Kendall 1983, Mattson et al. 1991). In years when cone production is poor, bears wander widely at lower elevations in search of food, and more often come into conflict with humans. This results in frequent management actions and higher bear mortality (Mattson et al. 1992). Whitebark pine communities have been designated critical habitat for grizzly bear recovery in the Greater Yellowstone Area and in other areas where recovery is planned (e.g., U. S. Fish and Wildlife Service 1997).

The hardiness of whitebark pine also promotes plant biodiversity in several ways. First of all, whitebark pine demonstrates fairly broad ecological amplitude with respect to its range (nearly 20° latitude and longitude), which encompasses different climates and orographic effects (Arno and Hoff 1990, Weaver 2001). Whitebark pine is also found on most aspects and on both moist and dry sites in parts of its range (Arno 2001). Within a region, whitebark pine may occur at different successional stages, as a climax, or as a krummholz community. Because understory

communities vary with successional stage, aspect, topography, latitude, and longitude, the collective plant biodiversity represented by whitebark pine communities is considerable. For example, in western Wyoming alone, 16 different whitebark pine habitat types have been identified, based on a moisture gradient from wet to dry (Arno 2001 and references therein).

Whitebark pine tolerates harsh, post-fire conditions, and with the aid of Clark's nutcracker is one of the first conifers to regenerate after severe fire, initiating ecological succession (Lanner 1980, Tomback 1986, Tomback et al. 1993, Tomback et al. 2001a). The seedlings provide favorable microsites for the establishment of less hardy conifers and herbaceous vegetation (Lanner 1980, Tomback et al. 1993). In fact, on harsher sites in the upper subalpine, whitebark pine may facilitate the establishment and survival of its competitors Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), acting as a "nurse tree" (Calaway 1998).

In addition to fostering biodiversity, whitebark pine provides other ecosystem services. Because it grows at the highest elevations of coniferous forest, tolerating steep, rocky, windswept sites where other conifers cannot survive, it both regulates runoff and reduces soil erosion. At these elevations, soils are poorly developed, with little capacity for water storage. The occurrence of trees at these high elevations slows snowmelt and regulates stream flows, which reduces flooding at lower elevations (Farnes 1990, Tomback et al. 2001b).

The decline of whitebark pine communities

Given the fact that 98% of whitebark pine communities are protected in wilderness area, national parks, and national forests, and occur at high elevations generally free from the development and disturbances prevalent around urban areas, it is astonishing that whitebark pine is seriously threatened by anthropogenic problems—exotic disease and advancing succession

from decades of fire suppression. The current status of whitebark pine reflects in part a synergism of natural and human-made causes. For example, major periodic outbreaks of mountain pine beetle from 1910 through the 1930's and in the 1970's and 1980's killed numbers of older, cone-bearing trees, and their skeletons still remain in many forests (Kendall and Keane 2001). Mountain pine beetle attacks appear again to be on the upswing, possibly the consequence of continuing drought (Six 2002). Advancing succession from fire suppression leads to larger trees and higher density stands, which are preferred by pine beetles because the trees may be stressed; blister-rust infected trees may be more susceptible to beetle attack, because they have lower resin flow and are thus less capable of fighting off beetles (Six 2002). Most critically, white pine blister rust is spreading and intensifying over time, although infection incidence varies greatly geographically and is less prevalent in arid regions, where conditions for spore production became less frequent.

To date, blister rust may be found nearly throughout the range of whitebark pine, with the exception of the Great Basin Ranges of Nevada and the southern Sierra Nevada; it is less prevalent at this time in the drier regions of the southern and eastern portions of the range (Smith and Hoffman 2000, Kendall and Keane 2001). Unfortunately, detailed information is lacking from a number of areas. But good survey information comes from the northern Rocky Mountains of the United States and southern Canada, where 10-50% of the whitebark pine are dead primarily due to blister rust, and an additional 35-100% of the trees are infected with blister rust (Keane et al. 1994, Kendall 1996, Stuart-Smith 1998, Campbell and Antos 2000, Zeglen 2002), and from the coastal ranges of British Columbia, where about 20-100% of the whitebark pine per stand are infected with blister rust (Campbell and Antos 2000, Zeglen 2002).

New assessments provide more information on the extent of blister rust infection. Recent work in the Selkirk Mountains of northern Idaho were consistent with the previous figures for the northern Rocky Mountains, with blister rust infection levels of 33-82%; some of these same trees were also attacked by pine beetles (Kegley et al. 2001). In the Greater Yellowstone Area, where blister rust was not expected to be a problem (Krebill and Hoff 1995), the disease has become more prevalent, particularly in the western and southern areas, where about 90% of the sampled stands had trees infected by blister rust, with an average infection incidence of 48% (Smith and Hoffman 2000). A recent survey in southwestern Oregon indicates an equally grim picture: 46% of all trees examined were infected by blister rust, with about 10% mortality primarily caused by blister rust (Goheen et al. 2002).

As whitebark pine communities decline over time, subalpine communities are projected to become more homogeneous with shade-tolerant conifers and more severe fire regimes (Tomback et al. 2001b, Keane 2001). Watershed protection will be lost locally, and the carrying capacity for bears, seed-eating vertebrates, and Clark's nutcrackers will decline. If nutcracker populations decline sufficiently, as their white pine food sources diminish, their seed dispersal services may well be lost (Tomback and Kendall 2001).

Restoration: a last chance

The outlook for the rich diversity of western five-needled white pine forests is particularly bleak with respect to maintaining historical patterns of community occurrence and structure on the landscape. Change in forest composition from the blister rust pathogen has been compounded by nearly a century of fire exclusion and periodic epidemics of mountain pine beetle (*Dendroctonus ponderosae*) (Kegley et al. 2001, Kendall and Keane 2001). The

disappearance of whitebark pine from the landscape, in particular, will have major ecological and biodiversity consequences.

In progress, however, are experimental programs to breed rust resistance in whitebark pine (Mahalovich and Dickerson 2001) for plantings in areas where seed source no longer exists, and to use both prescribed burning and silvicultural treatments to restore successional advanced whitebark pine communities on a relatively small scale (Keane and Arno 2001). This dual approach should serve as a model for the restoration of all five-needled white pine communities in the West, but time is growing short for action.

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Table 1. Average percentages of trees infected by white pine blister rust (*Cronartium ribicola*) (of live trees surveyed, either per stand or per population) in the northern range of whitebark pine (*Pinus albicaulis*). These figures do not include mortality rates from blister rust, which are highest in the northern Rocky Mountains of the United States.

Geographic region	Range of infection	Overall rate	Sample size	Years sampled	References
<u>United States, Rocky Mountains</u>					
Northern	0 – 100%	84%	307 stands	1990 - 1996	Keane and Arno 1993, Keane et al. 1994, Kendall et al. 1996
Central	0 – 62%	10%	129 stands	1995 - 1996	Kendall et al. 1996
<u>Canada, Rocky Mountains</u>					
Southern	27 – 76%	59%	9 stands	1996	Stuart-Smith 1998
	34 – 45%	38%	7450 trees	1998 - 2000	Zeglen 2002
Central	0 – 56%	17%	14 stands	1996	Stuart-Smith 1998
Northern	0 – 40%	17%	9 stands	1996	Stuart-Smith 1998
	44 – 52%	48%	578 trees	1998 - 2000	Zeglen 2002
Intermountain					

Table 1, page 2

Geographic region	Range of infection rates	Overall rate	Sample size	Years sampled	References
<u>Canada, Coast Ranges</u>					
Southern	11 – 28%	21%	3938 trees	1998 - 2000	Zeglen 2002
Central	20 – 21%	21%	2999 trees	1998 - 2000	Zeglen 2002
Northern	34 – 41	36%	1992 trees	1998- 2000	Zeglen 2002