

INVASIVE PATHOGENS AT ALPINE TREELINE: CONSEQUENCES FOR TREELINE DYNAMICS

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Abstract: The potential impact of invasive forest pathogens on alpine treeline dynamics has not previously been considered. Whitebark pine (*Pinus albicaulis*), a foundation and keystone species of subalpine forests and major component of alpine treeline in the northern Rocky Mountains of the United States and southern Canada, is infected nearly range-wide by the exotic pathogen *Cronartium ribicola*, which causes white pine blister rust. A major component of treeline in the northern Rocky Mountains, whitebark pine initiates tree islands on the eastern slope in northwestern Montana more than any other conifer species. Blister rust infects whitebark pine throughout the region, and both infection and mortality are already evident at treeline. We discuss the cascading ecological effects of the loss of treeline whitebark pine and expected changes in landscape vegetation patterns. Potential implications of the loss of whitebark pine for northwestern Montana treelines are examined in the context of climate change within a conceptual model. We speculate that exotic pathogens could potentially confound predictions of treeline responses to global warming in many geographic regions. [Key words: alpine treeline, whitebark pine, white pine blister rust.]

INTRODUCTION

The introduction of exotic pathogens is potentially a profound agent of change for forest landscapes worldwide (Holdenreider et al., 2004). Growing economic globalization and increased human mobility have enabled the worldwide spread of plant and animal pathogens and pests, despite increasing vigilance (e.g., Coblentz, 1990; Vitousek et al., 1996). In recent history, introduced diseases—and particularly fungal pathogens—have altered entire forest ecosystems by eliminating or severely diminishing important tree species. These forested landscapes now differ in structure, composition, and function with respect to their historical condition. For example, in the United States, Appalachian forests were co-dominated by oak (*Quercus* spp.) and chestnut (*Castanea dentata*) for thousands of years. In the late 1800s, the introduction of chestnut blight (*Cryphonectria parasitica*) from Asia to both Canada and the United States altered forest structure and fundamental ecosystem processes; within decades in the eastern U.S., chestnuts were replaced by oaks and eastern hemlock (*Tsuga canadensis*; Paillet, 2002; Jacobs and Severeid, 2004;

Ellison et al., 2005). European chestnut (*C. sativa*) has been similarly infected by the blight. Dutch elm disease, caused by the fungal pathogen *Ophiostoma ulmi* and later by *Ophiostoma novo-ulmi* and spread by elm bark beetles, was first detected in northwest Europe (probably with Asian origins) around 1910 and then arrived in North America sometime prior to 1930, resulting in continent-wide losses of native elms (Brasier, 1996; Haugen, 1998).

The highly invasive *Phytophthora* pathogens have been particularly destructive worldwide. In 1952, the exotic root pathogen *Phytophthora lateralis*, previously known from ornamental trees and suspected to originate in Asia, was found in Port-Orford-cedar (*Chamaecyparis lawsoniana*), which inhabits a small range in southwestern Oregon and northwestern California. All age classes of Port-Orford cedar have proven vulnerable to the disease, and riparian populations have been particularly susceptible (e.g., Roth et al., 1987; Sniezko et al., 2004). Sudden oak death, caused by the fungus *Phytophthora ramorum*, has achieved epidemic status in several oaks and tanoak (*Lithocarpus densiflora*) in California and Oregon (Meentemeyer et al., 2004). At least 23 plant species from 12 families may serve as host to this disease. Jarrah dieback, caused by the root pathogen *Phytophthora cinnamomi*, occurs throughout southern Australia and infects more than 40% of the native plants in the region (Weste and Marks, 1987). The disease was first discovered in Sumatra in the 1920s on cinnamon trees. Recent genetic sequencing suggests that *Phytophthora* pathogens have undergone rapid genetic divergence in proteins mediating specialized host interactions, and major diversification in plant toxins (Tyler et al., 2006). Furthermore, there is some evidence that infection severity by many of these pathogens increases under conditions of milder winters or higher temperatures in general (Harvell et al., 2002).

By extrapolation, exotic, invasive plant disease could potentially cause drastic changes in vegetation structure and composition in alpine environments. Although the position of treeline is determined by complex interactions among many variables at multiple spatial scales of influence (Malanson et al., 2007, in this issue), alpine treeline in particular has been the focus of attention for its potential as a bio-indicator of climate change (e.g., Innes, 1991; Rochefort et al., 1994; Körner, 1998). Researchers have detected responses of alpine treeline to warming and cooling trends in global climate through upslope or downslope movement of the ecotone, respectively, since the last glacial maximum (e.g., Rochefort et al., 1994; Lloyd and Graumlich, 1997). Modeling efforts have predicted the future response of treelines to climate warming scenarios as shifts upslope in the distribution of trees and tree islands (e.g., Grabherr et al., 1995; Hall and Fagre, 2003). However, even the most comprehensive studies and modeling efforts of alpine environments have not considered the confounding factors resulting from the direct and indirect effects of invasive pathogens.

Most research on invasive species has focused on ecosystems below alpine treeline. Some researchers cite a distinct elevation gradient associated with the distribution of invasive species in the western United States, with the majority of invasive species found at low elevations (e.g., Carolin et al., 2007; Fagre, 2007). Likewise, in New Zealand, reportedly few exotic species have become established in alpine regions (Halloy and Mark, 2003). Few invasive species are likely to be

adapted to the harsh year-round conditions and short growing seasons represented by high elevation environments. Similarly, invasive diseases and pests that are able to complete their life cycles at treeline elevations are rare.

The potential detrimental consequences of exotic, invasive disease at treeline should not be underemphasized simply because there are few known examples at high elevations. Forest pests and pathogens are among the most pervasive and important agents of disturbance in North American forests (Logan et al., 2003; Holdenrieder et al., 2004), and exotic invasive pests and pathogens may be even more devastating to ecosystems where invasions are uncommon (Allen and Kupfer, 2001). Such invasions may lead to significant alterations in ecosystem processes, which prevent recovery to predisturbance conditions (Orwig and Foster, 1998). Furthermore, invasive diseases at alpine treeline, in particular, have the potential to confound treeline dynamics, especially in context of climate change and biodiversity.

The dramatic decline of whitebark pine (*Pinus albicaulis*, Family Pinaceae) and the consequences for forest biodiversity, community development, species interactions, and local hydrology in the western United States and Canada provide a compelling illustration of the problem of invasive disease for alpine treeline. *Cronartium ribicola*, an exotic, invasive fungus that causes white pine blister rust (WPBR) is killing whitebark pine, a foundation and keystone conifer found in alpine treeline and subalpine ecosystems of the western United States. Although WPBR has been widely documented in subalpine whitebark pine communities nearly rangewide, and studied in both whitebark pine and related pines, it has been found to be prevalent within the alpine treeline only recently (Resler and Tomback, 2008). Thus, despite suggestions by researchers that dry, cold environments could inhibit the spread of the disease (e.g., Campbell and Antos, 2000), blister rust has successfully moved both to the northernmost limits of whitebark pine, about 55°N (Campbell and Antos, 2000; Zeglen, 2002; Smith et al., 2008), and to treeline (Resler and Tomback, 2008). Apparently, the harsh conditions in these regions do not prevent the rust either from completing its life cycle, or effecting transmission.

Mortality of whitebark pine at treeline from infection by the blister rust pathogen will have important implications with respect to the following factors: (1) whitebark pine is a treeline forest component throughout much of the northern Rocky Mountains; (2) the treeline community, including whitebark pine, is at the climate change "front" in the Rocky Mountains, and is expected to respond to global warming by moving up in elevation; (3) whitebark pine is a foundation and keystone species, and declines in this species will result in losses of ecosystem services, reduced community stability, and diminished biodiversity. The overarching question addressed by this paper is whether an invasive, exotic disease WPBR, could confound predictions of treeline dynamics in response to climate change. We address this question by presenting a conceptual model, which may be a starting point for predicting how other ecosystems could be affected by exotic, invasive pathogens.

WHITEBARK PINE AND *CRONARTIUM RIBICOLA*: BIOGEOGRAPHY, ECOLOGY, AND INTERACTION

Whitebark Pine

Whitebark pine is a foundation and keystone species of upper subalpine forest communities and the alpine treeline ecotone (Tomback, Arno, and Keane, 2001; Ellison et al., 2005). Foundation species are prominent members of ecological communities and greatly influence biodiversity, ecosystem processes, and stability (Soulé et al., 2003; Ellison et al., 2005). Keystone species, as currently defined, have greater effects on biodiversity than their abundance would suggest (Krebs, 2001; Soulé et al., 2003). In many forested ecosystems, foundation and keystone species locally stabilize both biotic and abiotic ecosystem components, creating conditions that are essential for other species and fundamental ecosystem processes such as water balance (Ellison et al., 2005).

Widely distributed throughout the high mountains of the western United States and Canada, whitebark pine occurs from about 37° to 55°N latitude, in the Pacific states and provinces from British Columbia south to the Sierra Nevada of California, and in the Rocky Mountains from Alberta south through the Salt River and Wind River ranges of western Wyoming (Arno and Hoff, 1990; Ogilvie, 1990; McCaughey and Schmidt, 2001). Whitebark pine inhabits most treeline communities within its range, except near its northern limits and in the snowiest northern regions, (e.g., coastal ranges of British Columbia); it is a dominant treeline component in the drier mountain ranges (Arno and Hammerly, 1984). It frequently assumes the krummholz growth form at the upper limits of alpine treeline, either as an individual (Fig. 1) or as a component of tree islands (Resler and Tomback, 2008).

Because of its role as both a foundation and keystone species in subalpine forests and at alpine treeline, the decline of whitebark pine from *Cronartium ribicola* has serious implications potentially for the ecosystems and biodiversity supported by this species (Tomback and Kendall, 2001; Schwandt, 2006; Tomback and Achuff, in review). Whitebark pine depends primarily on Clark's nutcracker (*Nucifraga columbiana*, Family Corvidae) for seed dispersal (Tomback, 1978, 1982; Hutchins and Lanner, 1982). Nutcrackers typically bury caches of 1 to 15 whitebark pine seeds throughout montane terrain from alpine tundra down to the lower forest treeline, transporting seeds as far as 12 to 22 km (Vander Wall and Balda, 1977; Tomback, 1978; see overview in Tomback, 1998). The seed cache sites selected by nutcrackers, coupled with seed and seedling requirements for germination and survival determine the distribution of the pine and genetic population structure on the landscape (Tomback and Linhart, 1990; Tomback, 2005).

Whitebark pine provides multiple ecosystem services (Tomback, Arno, and Keane, 2001; Ellison et al., 2005). The large seeds of whitebark pine comprise an important wildlife food for granivorous birds and mammals, including grizzly (*Ursus arctos*) and black bears (*Ursus americanus*), which rely heavily on whitebark pine seeds prior to hibernation (Kendall, 1983; Mattson and Reinhart, 1994; Tomback and Kendall, 2001). Whitebark pine seedlings are unusually robust and tolerant of stressful conditions (e.g., McCaughey and Tomback, 2001); the seedlings



Fig. 1. A whitebark pine grows in a sheltered microsite in the immediate lee of a boulder at alpine treeline near Divide Mountain, Blackfeet Indian Reservation, Montana.

establish rapidly after a burn and often grow at the highest elevations of any associated conifers (Tomback, 1986; Tomback, Anderies, et al., 2001; Mellmann-Brown, 2005). Consequently, whitebark pine facilitates community development, mitigating harsh conditions and favoring the growth of shade-tolerant competitors (e.g., Callaway, 1998). In the upper subalpine forests and treeline ecotone, whitebark pine stabilizes soil by reducing erosion; spreading pine canopies shade large areas and regulate the rate of snow melt downstream flows (Farnes, 1990; Tomback, Arno, and Keane, 2001).

Blister Rust Biology

The spread of *Cronartium ribicola* has caused the decline of five-needle white pine (Genus *Pinus*, Subgenus *Strobus*) forest communities in many regions throughout the West, infecting commercially valuable pines as well as high elevation species (McDonald and Hoff, 2001; Hunt, 2003; Tomback and Achuff, in review). Whitebark pine, one of the most severely impacted five-needle pines, is experiencing declining populations nearly rangewide from the pathogen (Kendall and Keane, 2001; McDonald and Hoff, 2001). For a growing number of regions, however, outbreaks of native mountain pine beetles (*Dendroctonus ponderosae*) in lodgepole pine (*Pinus contorta*) in response to climate warming are also killing vast numbers

of whitebark pine (Logan and Powell, 2001; Gibson, 2006; Taylor et al., 2006). In fact, the blister rust weakened trees are targeted by the pine beetle (Six and Adams, 2007).

Blister rust causes the loss of cone-bearing branches years before the tree dies (McDonald and Hoff, 2001), although seedlings and saplings may be killed within a few years of initial infection (Tomback et al., 1995). The northern Rocky Mountains of the United States, including northern Idaho and Montana, have the highest whitebark pine infection and mortality incidence from white pine blister rust of any other region, with average infection levels ranging from about 70 to 90%, (Kendall and Keane, 2001; Zeglen, 2002; Schwandt, 2006; Smith et al., 2008; Tomback and Achuff, in review). However, in this region, treeline krummholz whitebark pine has been surveyed only incidentally (e.g., C. M. Smith, pers. comm., 2007, Parks Canada, Waterton Lakes National Park, Alberta, Canada).

White Pine Blister Rust in the North American West

The white pine blister rust pathogen, native to Asia, was accidentally introduced in 1910 to western North America in the vicinity of Vancouver, British Columbia. The pathogen's life-cycle alternates between five-needle white pines and shrubs of the genus *Ribes*, comprising gooseberries and currants (Family Grossulariaceae; Mielke, 1943; McDonald and Hoff, 2001). The disease is perennial in host pines, ultimately causing damage and death. In alternate hosts, the disease lasts only a single growing season since leaves are shed in the fall. Recently, the genera *Pedicularis* and *Castilleja* (Family Orobanchaceae) were also found to serve as hosts (McDonald et al., 2006).

The life cycle of *Cronartium ribicola* involves five different spore types, several requiring 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; these hardy spores were determined to be blown as far as 500 km in the early years of pathogen spread (Mielke, 1943). In late summer, basidiospores produced on the alternate hosts transmit the fungus short distances to pines, thus completing the life cycle. Basidiospores infect pines through the needle stomata, and mycelia grow through the vascular tissue of the needle into the stem of the tree (Mielke, 1943). 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. The typically shrubby tree form of whitebark pine on all but the most favorable growing sites (e.g., Arno and Hoff, 1990) results in the canopy providing a large infection target for spores. Consequently, branch cankers tend to predominate in infected individuals (e.g., GYWPMWG, 2007; Smith et al., 2008). 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 (McDonald and Hoff, 2001).

Frequent favorable conditions for spore production and transmission enabled the blister rust pathogen to spread rapidly throughout the Pacific Northwest and Intermountain West of both the United States and Canada (Kendall and Keane, 2001; McDonald and Hoff, 2001). Countermeasures were pursued, including *Ribes*

eradication programs and fungicides, but provided little control (Bingham, 1983; McDonald and Hoff, 2001). By 2003, blister rust had spread to the northern extent of five-needle white pines in British Columbia and Alberta, as far east as the Black Hills of South Dakota, and into southern New Mexico (Hawksworth, 1990; Lundquist et al., 1992; Campbell and Antos, 2000; Zeglen, 2002; Blodgett and Sullivan, 2004). The trend for blister rust in the West has been geographical spread and local intensification; even in the absence of climate warming, this trend will continue (Schwandt, 2006; Tomback and Achuff, in review).

The Role of Whitebark Pine at Alpine Treeline in the Rocky Mountain Front

For much of its range in the Rocky Mountains, whitebark pine is a major component of tree island communities along the northern Rocky Mountain Front of Canada and the United States. For two study sites in northwestern Montana (48°N), Resler and Tomback (2008) found that almost all (95.8%) tree islands contained at least one whitebark pine, and the number of whitebark pine trees in tree islands with multiple trees ranged from 1 to 18. Among all solitary conifers examined, 67% were whitebark pine. The majority of the sampled whitebark pine had assumed a krummholz growth form, and appeared to be restricted in vertical height by extreme climatic conditions (Resler and Tomback, 2008).

We recently extended our field observations to the northern and southern limits of whitebark pine in the Rocky Mountains (Chipman et al., 2007). We examined the prevalence of whitebark pine in the treeline ecotone on the Beartooth Plateau, Wyoming (44–45°N) and in Kootenay and Banff national parks, British Columbia and Alberta, Canada, respectively (51°N). At both ends of its Rocky Mountain range, whitebark pine comprised an important component of the treeline community, occurring both as solitary individuals and in multi-species tree islands.

One tenant of landscape ecology is that local scale processes often explain landscape dynamics and patterns (Allen and Starr, 1982; Turner et al., 2001). This appears to be the case within the alpine treeline ecotone of the Rocky Mountain Front of northern Montana—one of the climatically harshest treeline environments in the northern Rockies—and to some extent in other Rocky Mountain treeline environments. In northern Montana, local processes of whitebark pine dispersal and establishment are in part responsible for generating landscape scale vegetation patterns. In this region, whitebark pine is not only a dominant conifer within treeline, frequently occurring even at the highest elevations of the ecotone (Resler et al., 2005), but is also the primary initiator of tree islands (Table 1; Resler, 2004; Resler and Tomback, 2008).

Among all treeline conifers in this region, whitebark pine most often grows in the immediate lee of microsites that mitigate the harsh treeline environment in this region (Resler, 2004; Resler and Tomback, 2008). Microsites such as terrace risers or boulders provide the safe sites for the germination and survival of conifers in this extreme environment (Butler et al., 2004; Resler et al., 2005). Once established, whitebark pine appears to facilitate the further establishment and growth of other conifers in its immediate lee (Callaway, 1998; Resler, 2004). In general, the establishment and survival of seedlings generates spatial pattern for tree islands at

Table 1. Results from Two Studies Showing Percent Occupancy of Initial Position (Position Immediately Adjacent to Shelter Source) by Conifers Found at Alpine Treeline in Tree Islands at Selected Sites in Northwestern Montana

Species	Resler (2004) ^a (%)	Resler and Tomback (2008) (%)
<i>Abies lasiocarpa</i>	23.0	18.0
<i>Juniperus communis</i>	6.0	2.0
<i>Juniperus horizontalis</i>	1.0	0.0
<i>Picea engelmannii</i>	24.0	14.0
<i>Pinus albicaulis</i>	39.0	64.5 ^b
<i>Pinus contorta</i>	5.0	0.0
<i>Pinus flexilis</i>	0.0	0.5
<i>Pseudotsuga menziesii</i>	2.0	1.0
n	128	259
Treeline Locations	Lee Ridge, Cataract Creek Basin, Divide Mountain	Lee Ridge, Divide Mountain

^aSampling quadrats at Lee Ridge and Divide Mountain different in location from Resler and Tomback (2008).

^bValue includes 5 tree islands where *Pinus albicaulis* occupied the initial position with another conifer species.

treeline (Hättenschwiler and Smith, 1999; Germino et al., 2002). Given the importance of these facilitation interactions in the northern Rocky Mountain Front of Montana, there is an especially strong connection in process between the establishment and survival of whitebark pine seedlings and tree island spatial pattern in this region.

Survival of whitebark pine seedlings in this continental treeline environment probably results both from the sheltered seed caching sites selected by Clark's nutcrackers and the hardiness of the seedlings (e.g., McCaughey and Tomback, 2001). Nutcrackers typically harvest whitebark pine seeds from the subalpine forest and transport seeds to treeline and even tundra for seed caching (Tomback, 1986; Baud, 1993). They cache seeds near sheltered sites at treeline, such as in the lee of trees, rocks, logs, and stumps (e.g., Tomback, 1978), microtopography, and edges of tree islands. These sheltered sites contribute to whitebark pine survival and ultimately to the spatial distribution of whitebark pine on the landscape. Seedlings not in sheltered sites or windward of rocks and vegetation have lower survival (e.g., Maher et al., 2005; Mellmann-Brown, 2005).

Sheltered sites clearly moderate harsh conditions that could cause seedlings to perish in critical early years (Butler et al., 2004; Resler et al., 2005). Sheltered sites can support seedling survival by providing shade and reducing wind damage caused by ice particle abrasion and desiccation (Marr, 1977; Benedict, 1984). Shade reduces extreme diurnal temperature fluctuations, which have been shown to kill conifer seedlings at alpine treeline (Germino et al., 2002). Shelter may also increase soil moisture by reducing incident solar radiation (Lamb and Chapman,

1943; Pérez, 1987, 1991), and by capturing and retaining snow (e.g., Alftine et al., 2003; Hiemstra et al., 2006). A protected microsite may also facilitate conifer root colonization by mycorrhizae (Hasselquist et al., 2005).

With whitebark pine as a tree island initiator, positive feedback mechanisms play an important role in further tree island development. The establishment of whitebark pine within a microsite increases the probability that a second seedling will become established to its lee. Most treeline conifers (Table 1) have wind-dispersed seeds; the exceptions are whitebark and limber pine (*Pinus flexilis*), which are primarily nutcracker dispersed, and *Juniperus* spp., which tend to be animal or gravity dispersed. Whitebark pine in the lee of a shelter may increase the probability of seed dispersal to the site (e.g., by catching blown seeds) and/or seedling survival. The survival of a second conifer may further facilitate the dispersal and establishment of additional conifers. Given the importance of site conditions in general, the availability of shelter, such as provided by microtopography, surface geomorphic features, or existing vegetation, will not only influence the spatial pattern of treeline vegetation development, but also influence patterns in treeline advance (Resler, 2006).

White Pine Blister Rust at Treeline

White pine blister rust is present nearly rangewide in whitebark pine, including at its northernmost limits (Campbell and Antos, 2000; Zeglen, 2002; Smith et al., 2008); thus, it is not surprising to find that blister rust has spread to whitebark pine within alpine treeline communities, particularly in regions where infection levels are highest. Resler and Tomback (2008) sampled within two study areas east of the Continental Divide, on the Blackfeet Indian Reservation and in Glacier National Park, a region where whitebark pine in the surrounding subalpine forest has the highest blister rust infection levels on record (Kendall and Keane, 2001), and found that blister rust infection was common (35% overall infection rate) in whitebark pine at treeline (Table 2). For study areas on the Beartooth Plateau and in Kootenay and Banff National Parks, Chipman et al. (2007), also found blister rust present, but at a lower incidence than in the northern Montana treeline study areas. Given the importance of whitebark pine to tree island formation in the northern Rocky Mountain Front, loss of whitebark pine to blister rust could potentially alter tree island distribution on the landscape and delay or inhibit treeline response to climate warming.

IMPLICATIONS OF WHITEBARK PINE MORTALITY WITHIN THE ALPINE TREELINE: A CONCEPTUAL MODEL

The question addressed by this paper is whether an invasive, exotic pathogen can confound predictions of treeline dynamics in response to climate change. We use whitebark pine and blister rust as a case study, based on our observations from the Rocky Mountain Front in northwestern Montana. We present a conceptual model (Fig. 2), which addresses the interactions among pathogen, host, climate,

Table 2. Whitebark Pine, Blister Rust Infection, and Whitebark Pine Mortality at Two Alpine Treeline Study Locations

Transect ID	Study site									
	Lee Ridge					Divide Peak				
	1	2	3	4	5	1	2	3	4	5
Number of tree islands	29	26	33	30	14	42	19	39	7	27
No. whitebark pine trees	17	25	38	27	10	42	20	35	16	24
% whitebark pine infected (potential, inactive and active cankers)	17.6	24.0	52.6	51.9	20.0	26.2	0.0	48.6	31.3	37.5
% whitebark pine infected (inactive and active cankers only)	5.9	20.8	20.8	48.1	10.0	14.2	0.0	40.0	31.3	20.8
No. dead whitebark pine trees (probable cause of death, blister rust)	1	1	0	3	1	2	0	3	0	2

Source: Resler and Tomback (2008).

and treeline, and could be generalized to treeline communities outside the range of whitebark pine.

Historical and Current Response of Whitebark to Climate Change at Treeline

Historical reconstruction indicates that as regional temperatures warm, western treelines advance in elevation; and, current analyses indicate a contemporary response to warming trends (e.g., Scuderi, 1987; Rochefort et al., 1994; Bekker, 2005). In the Sierra Nevada, whitebark pine has demonstrated a response to 20th century warming by advancing into previously unoccupied snowfields, increasing branch growth, and experiencing vertical branch growth in previously krummholz growth forms (Millar et al., 2004). In general, tree-ring chronologies of whitebark and other high elevation five-needled white pines as well as associated conifers exhibit higher growth rates during the last half-century than the previous 1000 years, which is interpreted as a signature of global warming trends (Bunn et al., 2005). As previously mentioned, recent bioclimatic models predict latitudinal shifts in whitebark pine distributions from south to north, and to higher elevations in the northern Rocky Mountains (Bartlein et al., 1997; Rehfeldt et al., 2006; Schrag et al., 2007).

Decline in Treeline Whitebark Pine (A in Fig. 2)

The pathogen *Cronartium ribicola* potentially limits the abundance and distribution of whitebark pine within the alpine treeline ecotone in two ways: First (1 in Fig. 2), WPBR is killing established whitebark pine trees in the treeline ecotone (Table 2; Resler and Tomback, 2008), thus reducing opportunities for facilitating the recruitment and establishment of other conifers. Second (2 in Fig. 2), as trees in the

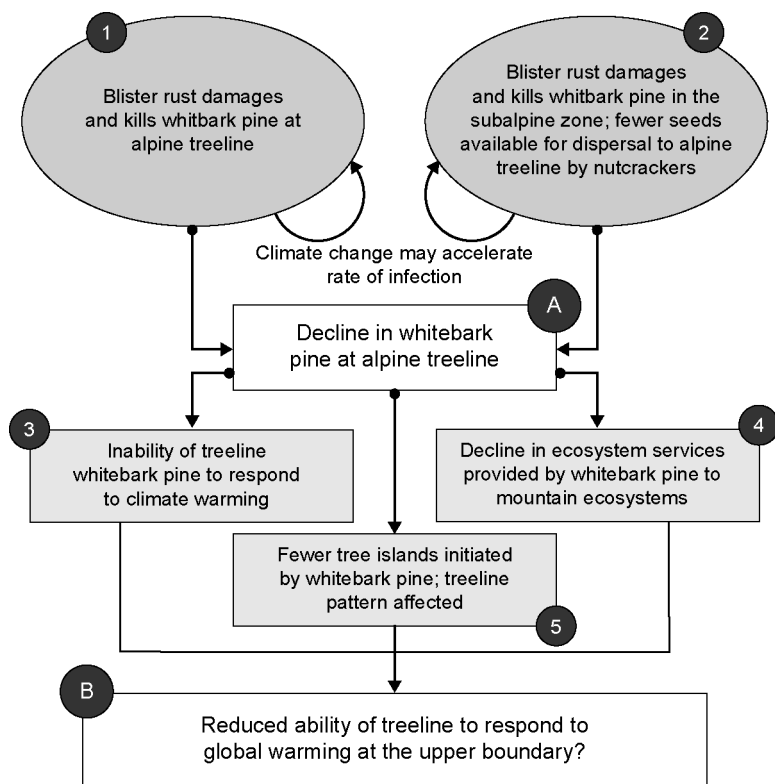


Fig. 2. A conceptual model of the central role of whitebark pine at treeline in terms of its interactions with blister rust.

subalpine forest zone below the treeline ecotone are infected and damaged by blister rust, they lose their ability to produce seeds, either through the progressive loss of living branches or by dying (e.g., Hoff et al., 2001; McKinney and Tomback, 2007), so that fewer seeds are available for nutcrackers to disperse to the alpine treeline ecotone (e.g., Tomback, 1986). With fewer healthy whitebark pine present at treeline over time, the pattern of tree island distribution and tree island development will be altered. Loss of single whitebark pine trees will lead to a reduction in absolute tree density at treeline, and concomitantly reduce the chances that multi-tree islands will be established.

Furthermore, the incidence of WPBR in subalpine forest whitebark pine and spread in both the alpine and the subalpine may be accelerated by climate warming, especially if cold temperatures and low humidity have previously limited spore production or transmission. The geographic spread of blister rust has been connected to “wave-years,” which are climatically suitable periods for spore production and transmission (Mielke, 1943). Climate change, particularly in precipitation patterns, may increase transmission rates, as modeled by Koteen (2002). Under these conditions, losses of whitebark pine in the subalpine forest and at treeline

may be greatly accelerated because of synergistic effects, since blister rust may reduce whitebark pines's stress tolerances or competitive responses. For example, mortality caused by blister rust hastens replacement of whitebark pine by more shade-tolerant conifers in successional communities (Keane et al., 1990; Keane, 2001). In general, climate has been shown to influence pathogen activity (Richardson and Bond, 1991) and global warming in particular has been predicted to influence the survival of pathogens, host susceptibility, and transmission rates (Harvell et al., 2002).

The damage and mortality in whitebark pine from blister rust at the two climate change fronts, i.e., northernmost distributions and alpine treeline, may counter tendencies toward northward or upward movements if tree island initiation is reduced in frequency. Thus, the effects of blister rust may be at landscape scale, impacting vegetation development and even countering global warming predictions.

Perceived Inability of Whitebark Pine to Respond to Global Warming (3 in Fig. 2)

If a high proportion of whitebark pine in the subalpine forest and at treeline succumbs to blister rust, then the response of whitebark pine to climate change at treeline becomes highly uncertain. First of all, research indicates that treeline whitebark pine will in fact respond to climate warming by establishing progressively farther upslope (e.g., Millar et al., 2004). However, if most whitebark pine that establish higher than current treeline are killed by blister rust, there will be little or no evidence of response to warming temperatures. Secondly, as whitebark pine seed sources decline within the subalpine forest, nutcrackers will disperse fewer seeds in general, and certainly fewer seeds above current treeline, further limiting potential whitebark pine establishment (McKinney and Tomback, 2007). In fact, whitebark pine in general will decline as a component in treeline communities even as climate warms. Unless the specific consequences of *Cronartium ribicola* were understood at the landscape level, i.e., its landscape pathology (Holdenrieder et al., 2004), the vegetation pattern on the landscape would indicate that whitebark pine is not responding to climate change.

Decline in Ecosystem Services Provided by Whitebark Pine to Mountain Ecosystems (4 in Fig. 2)

As whitebark pine is damaged and killed by blister rust within subalpine forests, the ecosystem services it provides, including its large, nutritious seeds as wildlife food, soil stabilization, and community development through facilitation interactions, are diminished, as are opportunities for natural regeneration (Tomback and Kendall, 2001; McKinney and Tomback, 2007). Furthermore, modeling shows that by killing whitebark pine, blister rust creates a more homogeneous spruce-fir forest, which in turn leads to more severe fire regimes (Keane et al., 1990; Keane et al., 2002). More severe fire regimes have economic implications, including the cost of fire suppression; loss of commercially valuable species; and soil erosion from uncontained run-off, as well as impacts on downstream water quality for agriculture.

The loss of whitebark pine at treeline also affects lower elevation ecosystems: Because whitebark pine tolerates harsh conditions, it occurs at the highest treeline elevations where tree islands develop and shade snowpack—a process that regulates alpine snowmelt and thus downstream flow (Farnes, 1990). As whitebark pine declines at treeline, flushes of snowmelt are likely (Farnes, 1990), resulting in lower stream flows late in summer. In addition, loss of whitebark pine at treeline reduces the density and distribution of treeline vegetation, which in turn may result in erosion of soil, with accumulation of sediments in streams. For northwestern Montana, we speculate that the projected loss of whitebark pine at treeline may reduce the density of treeline vegetation. This represents loss of habitat for wildlife, and particularly for species that live in the treeline ecotone, including small mammals and birds.

Fewer Tree Islands Initiated by Whitebark Pine: Treeline Pattern Affected (5 in Fig. 2)

As described above, whitebark pine helps shape the pattern of tree island vegetation on the landscape through its abundance at treeline and through facilitating the establishment of multi-tree islands. With blister rust reducing the prevalence of whitebark pine, the following changes to current vegetation patterns on the landscape are possible: Many solitary whitebark pine will die before they are able to facilitate the establishment of a second conifer, limiting the future potential for multi-tree tree islands and reducing the distribution and abundance of treeline ecotone conifers. As whitebark pine leeward to sheltering microsites succumb, conifers to their leeward may become stressed, triggering a wave of mortality within a tree island. The process of tree island development, such as the “infilling” of trees around and between existing tree islands (Bekker, 2005) may be limited or delayed, since whitebark pine occurs primarily as solitary trees at treeline (Resler and Tomback, 2008). Other conifer species may become established over time in some suitable shelter sites, and possibly facilitate the establishment of multi-tree tree islands and contribute to infilling; this will alter community structure and composition. Whether this occurs depends on the likelihood of seed dispersal and seedling establishment for these other conifers in the harsh climate of the Rocky Mountain Front.

At higher and lower latitudes in the Rocky Mountains, where whitebark pine is abundant at treeline, but less important as a tree island initiator (Chipman et al., 2007), blister rust will reduce the density and alter the pattern and composition of treeline vegetation on the landscape. Solitary whitebark pine trees are important in these regions as well, and whitebark pine seedlings are still hardier and more able to establish on harsh sites than associated conifers (e.g., Mellmann-Brown, 2005).

Reduced Ability of Treeline to Respond to Global Warming at the Upper boundary? (B in Fig. 2)—Confounding Factors of Climate Change and Blister Rust at Alpine Treeline

As described for process 3 in Figure 2, continuing or accelerating mortality of whitebark pine from blister rust will prevent or greatly restrict whitebark pine from

becoming established above current treeline limits, even as climate warms. The reduced presence of whitebark pine and reduced facilitation will limit the ability of other conifers to respond to global warming either indefinitely, or may at least lengthen the timeframe of response. Although whitebark pine is the most frequent initiator of tree islands at the highest elevations of trees throughout our northern Montana treeline study areas, other species of conifers do initiate tree islands (Table 1), under suitable conditions.

With the current trajectory of climate warming, other species could replace whitebark pine in initial tree island establishment at the highest extent of the ecotone, but with considerable lag time. Warming may need to progress considerably before other conifers are able to survive above current treeline. Ultimately, the advancing treeline ecotone may remain sparsely colonized, and show inevitable changes in species composition. It is also possible that treeline elevation will not rise as climate warms.

Thus, given predictions that the distribution of whitebark pine will shift northward and to higher elevations at the current rate of climate warming (e.g., Rehfeldt et al., 2006), the upper extent of the treeline ecotone may, instead, lose whitebark pine. Ultimately, for whitebark pine, the ability of this species to move upward in response to climate warming may determine how long it will remain part of the western United States forest landscape. For the northern Rocky Mountains of the United States, by 2030 the climate for all but the highest elevations is predicted to be unsuitable for whitebark pine (M. Warwell, pers. comm., 2006, USDA Forest Service, Rocky Mountain Research Station, Moscow, Idaho). We must be cautious in interpreting these predictions: some established trees could persist as long as centuries—but with lower likelihood in the presence of blister rust.

General Application of Model to Other Treeline-Pathogen Interactions

The specific influence of *Cronartium ribicola* in alpine treeline dynamics has the potential to confound global warming impacts throughout all treeline ecotones where five-needle white pines are present. Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) are two five-needle high-elevation pines that are important treeline species throughout several western regions (e.g., Baker, 1992; Schoettle, 2004). Both species are infected by blister rust in parts of their range (Blodgett and Sullivan, 2004; Tomback and Achuff, in review). Studies are needed to determine the general importance of these species in generating vegetation pattern at treeline, but preliminary observations of bristlecone pine suggest that it may initiate tree islands in parts of its northern range (A. W. Schoettle, pers. comm., 2006, USDA Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado). Therefore, blister rust may well affect treeline dynamics across a broad geographic range. With blister rust killing whitebark pine and other five-needle treeline conifers, the response of treeline to climate change in the Rocky Mountains may now be more complex than simple distributional shifting.

The conceptual model presented here by no means is limited to the influence of *Cronartium ribicola* on five-needle white pines. Any pathogen that has the capacity to kill or weaken a dominant or foundation (sensu Ellison et al., 2005) tree species

that inhabits the treeline ecotone has the potential to complicate predicted treeline response to climate warming. For example, exotic pathogens may emerge which impact *Nothofagus* spp. treeline forests in New Zealand or Patagonia, or other important tree species (e.g., *Pinus sylvestris*, *Picea abies*, and *Betula pubescens* at both arctic and alpine temperate zone treelines).

CONCLUSION

Researchers are just beginning to understand the serious consequences of invasive, exotic disease in ecosystems throughout the world (Harvell et al., 2002; Holdenrieder et al., 2004). The potential for invasive, forest pathogens to disrupt vegetation patterns at treeline, as they do at lower elevations, is abundantly clear (e.g., Meentemeyer et al., 2004; Ellison et al., 2005). However, with climate warming as an added factor, the magnitude and outcome of disrupted patterns and species interactions cannot be entirely predicted. In fact, increased severity of infection with warming temperatures has been documented for a number of invasive plant diseases (Harvell et al., 2002). The potential impacts of invasive pathogens raise the following general questions: Will treeline community composition and dynamics change with time, with the spread of invasive disease? How will disease manifestation change in response to climate warming? How will the new vegetation pattern respond at treeline as temperature increases?

Losses of a dominant or foundation treeline species to a pathogen may result in changes in vegetation pattern on the landscape that are contradictory to projected impacts of global warming. Invasive pathogens can thus be added to the list of factors, including local geomorphology, topography, historic cultural influences, regional climate, and local climate, that result in an idiosyncratic response by the local treeline community to global warming (Holtmeier and Broll, 2007; Malanson et al., 2007, in this issue). In other words, in the presence of an introduced pathogen, absence of upward movement of alpine treeline on a mountain slope does not necessarily indicate an absence of the effect of climate change on vegetation.

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