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Blister Rust Prevalence in Krummholz Whitebark Pine: Implications for Treeline Dynamics, Northern Rocky Mountains, Montana, U.S.A.

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Abstract

Whitebark pine (*Pinus albicaulis*), an important treeline conifer in northern Montana, is considered both a keystone and foundation species in high-elevation ecosystems. The introduced fungal pathogen *Cronartium ribicola*, which causes white pine blister rust, has resulted in severe declines in whitebark pine in subalpine forest communities throughout the northern Rockies during past decades. However, the prevalence of blister rust in whitebark pine within the alpine treeline community and its impact remain to be determined. We gathered field data on blister rust infection incidence in the treeline ecotone at two locations east of the Continental Divide in the northern Rocky Mountains, Montana, U.S.A. Our objectives were (1) to examine the potential importance of whitebark pine in tree island formation, (2) to determine if blister rust is present in whitebark pine within the alpine treeline community, and (3) to characterize the incidence and intensity of blister rust in krummholz tree islands. We found that whitebark pine is the primary initial colonizer in tree island formation, indicating that the species is important in generating vegetation pattern in these communities. Thirty-five percent of all sampled whitebark pine were infected with blister rust. Although more cankers were found in solitary whitebark pine trees, highest infection incidence per tree occurred in trees that were part of multitree islands. Finally, we found a significant correlation between tree island length and infection incidence. These results have important implications with respect to alpine treeline dynamics on a landscape scale, especially in the context of climate change.

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Introduction

Ecologists and biogeographers 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). Given that certain species have disproportionate effects on community structure and biodiversity, exotic disease can potentially result in a trophic cascade, seriously disrupting community composition and species interactions. For example, foundation species are prominent members of ecological communities, either by structure or function, 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). The loss of keystone or foundation species to exotic disease could lead to a drastic reduction of biodiversity or even functional collapse within an ecosystem.

Whitebark pine (*Pinus albicaulis*), an upper subalpine forest and treeline conifer widely distributed throughout the western United States and Canada (Arno and Hoff, 1990; Ogilvie, 1990; McCaughey and Schmidt, 2001), serves both as a foundation and keystone species, providing multiple services (Tomback et al., 2001a; Ellison et al., 2005). Whitebark pine depends primarily on Clark's nutcracker (*Nucifraga columbiana*) for seed dispersal (Tomback, 1978; 1982; 1986; Hutchins and Lanner, 1982; Tomback and Linhart, 1990). Nutcrackers typically bury whitebark pine seeds in caches of 1 to 15 seeds throughout mountainous terrain, including recent burns, from the alpine treeline ecotone down to the lower treeline, transporting seeds as far as 12 to 22 km (Vander Wall and Balda, 1977; Tomback, 1978; Tomback, 1998). The large, wingless seeds of whitebark pine comprise an important wildlife food for other granivorous birds and mammals as well, 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; the seedlings establish rapidly after fire and grow at the highest elevations of any associated conifers (Tomback, 1986; Tomback et al., 2001b). Consequently, whitebark pine can facilitate community development, mitigating harsh conditions, and the establishment of more shade tolerant competitors (e.g., Callaway, 1998). In the upper subalpine forests and treeline ecotone, whitebark pine stabilizes substrate, reducing erosion; the spreading pine canopies shade large areas, reducing the rate of snow melt and regulating downstream flows (Farnes, 1990; Tomback et al., 2001a).

Previously, Resler (2004) suggested that whitebark pine in the treeline ecotone east of the Continental Divide may be the most frequent conifer to initiate tree islands, primarily due to the selection of sheltered seed caching sites by Clark's nutcrackers, as well as the hardiness of the seedlings. These sheltered sites are important for whitebark pine survival and account in part for the spatial distribution of whitebark pine on the landscape. The presence of whitebark pine in a sheltered site further mitigates the harsh conditions and facilitates the survival of additional, less hardy conifers, thus building tree islands.

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Whitebark pine populations in upper subalpine forests are declining nearly rangewide from infection by the exotic fungal pathogen *Cronartium ribicola*, which causes the disease white pine blister rust in five-needled white pines (Kendall and Keane, 2001; McDonald and Hoff, 2001; Schwandt, 2006). The blister rust enters the stomata of pine needles, and mycelia grow down through the cambium of twigs, branches, and stems, producing sporulating cankers after several years. These cankers damage the living cambium, which eventually kills the branch or stem. Blister rust infection often 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). This exotic pathogen has serious implications not only for the survival of whitebark pine, but also potentially for the ecosystems and biodiversity supported by whitebark pine (Tomback and Kendall, 2001; Schwandt, 2006; Tomback and Achuff, submitted). However, researchers have suggested that "the spread of the disease may be limited in dry, cold environments" (e.g., Campbell and Antos, 2000), because some stages of the blister rust life cycle require high relative humidity and mild temperatures. Given the aridity and extreme cold of the alpine treeline ecotone, white pine blister rust should not be widespread in these ecosystems. However, little is known about the incidence and intensity of white pine blister rust within the treeline ecotone.

In the northern Rocky Mountains of the United States, including northern Idaho and Montana, whitebark pine in the subalpine forest below treeline has the highest infection and mortality incidence from white pine blister rust of any other region, with average infection levels about 70% and infection levels on individual plots as high as 100% (Kendall and Keane, 2001; Schwandt, 2006; Smith et al., 2008). However, in this region, treeline krummholz whitebark pine has been surveyed only incidentally (e.g., C. M. Smith, pers. comm.). In October 2005, we observed that blister rust infection was common in whitebark pine krummholz in the alpine treeline ecotone east of the Continental Divide on the Blackfeet Indian Reservation in northwestern Montana, U.S.A., an area where whitebark pine in the surrounding subalpine forest has among the highest blister rust infection levels on record (Kendall and Keane, 2001). Treeline climate in this region is very cold, windy, and arid and exacerbated by the widely fluctuating extremes of continental climate (Finklin, 1986).

We returned to northwestern Montana in summer 2006 to examine the ecological implications of blister rust in the treeline ecotone, particularly in relation to treeline dynamics. In this study, we confined our investigation to two study sites within a defined geomorphic and climatic zone east of the Continental Divide in northern Montana. The objectives of this study were (1) to examine the potential relationship between the establishment of whitebark pine and krummholz tree island formation, (2) to determine whether blister rust is in fact present in treeline ecotone whitebark pine , and (3) to determine the incidence and intensity of blister rust in whitebark pine, both isolated and within krummholz tree islands, at both locations within this defined geographical region.

Methods

STUDY AREAS

We sampled whitebark pine at the altitudinal treeline in two study sites on the eastern side of the Continental Divide in windswept periglacial environments, at elevations ranging from 2050 to 2150 m (Fig. 1). Lee Ridge (48°92′N, 113°65′W), located within the boundary of Glacier National Park, is an isolated ridge located about 100 km southwest of Lethbridge, AB, Canada; Divide Peak (48°67′N, 113°38′W), situated on the border of the Blackfeet Indian Reservation and Glacier National Park, lies about 10 km south of St. Mary, Montana, U.S.A. The Divide Peak area becomes increasingly wind-exposed farther away from the base of the actual peak. Locations east of the Continental Divide are characterized by climate that is drier, windier, and cooler than climates west of the Continental Divide (Finklin, 1986; Walsh et al., 1992), even at treeline elevations.

Our study sites are characterized by roughly parallel terrace treads and risers, which are step-like, linear, patterned-ground formations created by accumulations of fine-grained material (Washburn, 1980; Butler and Malanson, 1989; 1999). Surface boulders that have been transported from cliff bases by the flow of previously active solifluction are found scattered throughout the landscape. Lee Ridge is an isolated, exposed ridge located perpendicular to the prevailing westerly winds. The Divide Peak site is located on inactive solifluction treads and risers at the base of an isolated peak at the easternmost boundary of the Rocky Mountain physiographic province (Resler et al., 2005).

Conifers, including whitebark pine, exist as multitree patches or isolated individuals, referred to here as "tree islands" (Marr, 1977) at the upper extremes of their elevational distributions. The patches are landscape elements distinct from the upper subalpine continuous forest cover. Whitebark pine typically occurs (sometimes in a krummholz form) in the higher elevations of the ecotone (Resler et al., 2005). The tree islands may contain as few as one individual or as many as several hundred, and range in length from a few centimeters (seedlings) to more than 35 m (large tree islands with multiple trees). In our treeline ecotone study sites, periglacial features such as terrace risers or boulders (Fig. 2) are important in the establishment of vegetation and conifer patches at these sites (Resler et al., 2005). Conifers establish in patches or as individuals within an alpine tundra matrix and are often found leeward of microtopographic features such as boulders, periglacial patterned ground, and topographic hollows that serve as shelter. Several different conifer species may be close spatial associates, and under less stressful conditions would not likely coexist. For example, *Pinus albicaulis, Pinus contorta*, and *Picea engelmannii* have been were found in close proximity within a single patch at Lee Ridge (Resler, 2004).

TREE ISLAND SAMPLING

Tree islands were sampled during the third week of July, 2006. One baseline 200 m long "vertical" transect, i.e., a transect parallel to the fall line, was established at each study site–on a NNW slope aspect on Lee Ridge and NE aspect at the base of Divide Peak. We placed these vertical transects in proximity to the most continuous elevational line of krummholz trees and tree islands on the slope. For both study sites, a blind toss of a transect pin determined the starting positions of the 200 m baseline transect.

For tree island sampling, we established five "horizontal" belt transects, i.e., transects perpendicular to the baseline elevational transect, at 50 m intervals crossing the 200 m vertical transect to delineate sampling boundaries. All sampling belt transects were parallel and followed the same compass bearing. Biophysical details sampled at each transect and data collected are listed in Table 1.

Due to differing densities of whitebark pine at each study site, belt transects at Lee Ridge were 75 m long × 10 m wide and at

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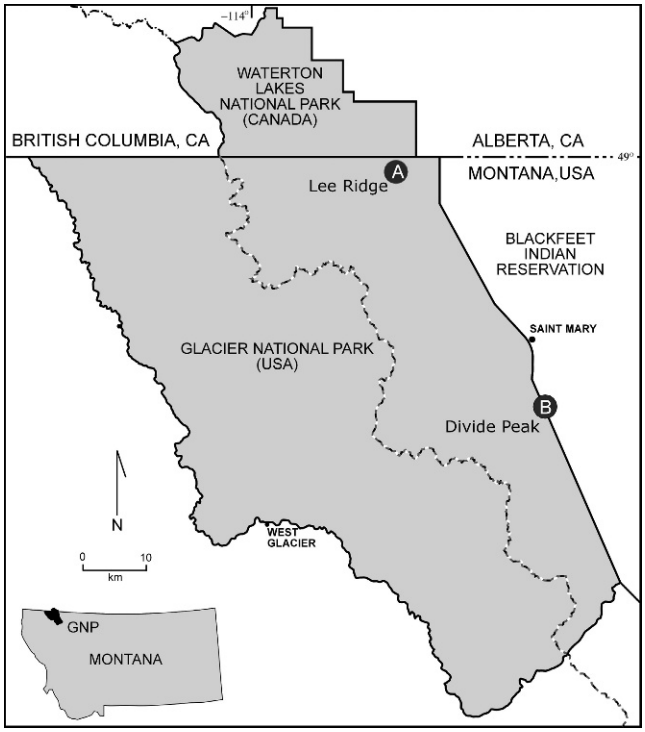


FIGURE 1. Map of Glacier National Park and surrounding areas, with location of study sites Lee Ridge (A), and Divide Peak (B). Dashed line indicates the Continental Divide.

Divide Peak, 50 m × 10 m, i.e., belts were extended 5 m on either side of each horizontal transect. The total area sampled at Lee Ridge was 3750 m^2 (number of tree islands, $n = 132$) and at Divide Peak was 2500 m^2 (number of tree islands, $n = 134$). For each belt transect, we recorded aspect, slope steepness, GPS positions of endpoints, and general site conditions.

We identified and classified all tree islands, regardless of age or size, that fell completely or partially within the belt transect as multitree or solitary-tree islands. Multitree islands were defined as those with more than one conifer in close spatial proximity (touching branches). Resler et al. (2005) reported that most tree islands were initiated adjacent to a shelter source, such as a rock, small topographic depression, or other vegetation on the windward side of the tree island. For each tree island, the shelter type was identified as one of the following: rock, vegetation, terrace riser, combination shelter, or no apparent shelter. Rocks were defined as prominent microtopographic, monolithic features associated with the periglacial landscape. We defined vegetation as a conifer or willow (*Salix* spp.) found immediately windward of another tree.

Vegetated terrace risers in northwestern Montana are associated with periglacial geomorphic processes, and are typically composed of fine-grained material vegetated primarily by *Dryas octopetala*. Slope of the risers ranges from about 2 to 20°, with 3 to 7° being the most common (Resler et al., 2005). Combination shelters are defined here as sites characterized by the dual sheltering effects of either turf-banked terrace risers and boulders, or terrace risers and vegetation.

Tree island composition, defined as the different species present within each conifer patch; longest dimension of each conifer patch; number of whitebark pine per tree island; and, starting and leeward conifer, were recorded for the purpose of determining the importance of whitebark pine as the initiating conifer for tree islands. In three instances, the areas of tree islands were in excess of 35 m^{-2}. For these cases, only the whitebark pines that fell within our sampling area were surveyed for blister rust. Limber pine (*Pinus flexilis*), a high elevation five-needled white pine that resembles whitebark pine, was also present in our sites. Although the two species may be distinguished by pollen and seed cones, none were produced; thus, we confirmed identification of whitebark pine using needle morphology (Kral, 1993). Finally, for the purpose of describing structural form, we categorized each whitebark pine tree as krummholz (low growing, wind-shaped trees that are often densely matted), flagged (trees with foliage primarily on one side indicating wind damage), or upright (fully erect). Given the extreme environmental stress on trees in our

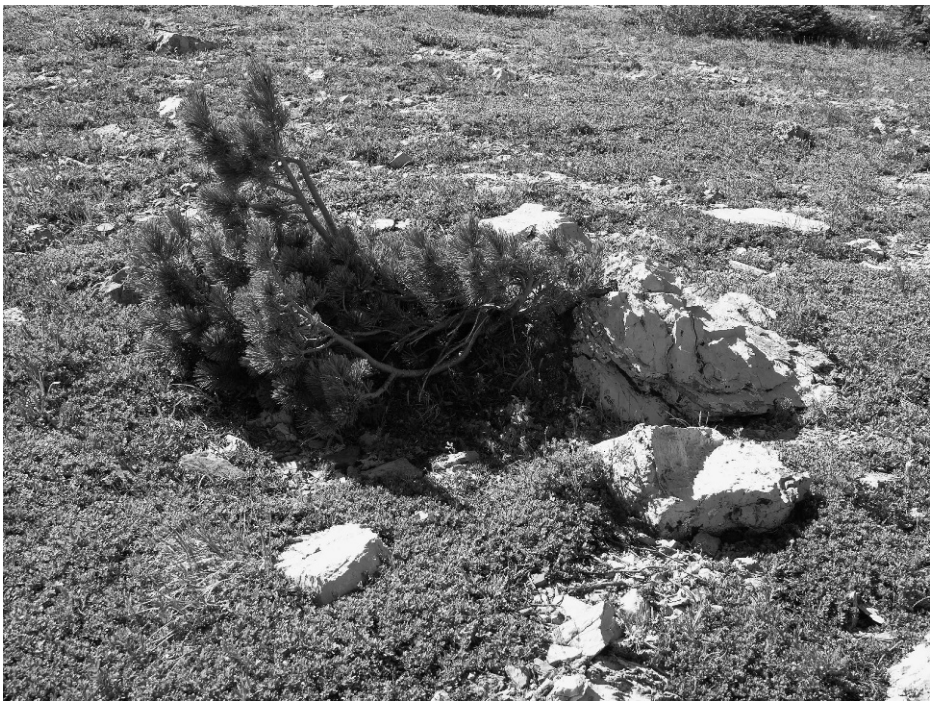


FIGURE 2. Whitebark pine growing in sheltered microsite in lee of boulder. Predominant wind direction is from the right (west) of the photo.

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TABLE 1

Description of transects and associated tree islands at Lee Ridge (LR) and Divide Peak (DP).

Study Site	Lee Ridge (75 m × 10 m transects)					Divide Peak (50 m × 10 m transects)				
Transect ID	LR1	LR2	LR3	LR4	LR5	DP1	DP2	DP3	DP4	DP5
Elevation (m)	2168	2167	2155	2159	2136	2097	2099	2114	2120	2127
Slope (°)	0	0	1	1	2–3	12–13	1	2	2	1–2
Aspect	NNW	NNW	NNW	NNW	NNW	NE	NE	NE	NE	NE
No. Tree Islands	29	26	33	30	14	42	19	39	7	27
Tree Island Density (per 1000 m^{-2})	38.6	34.6	44.0	40.0	18.6	84.0	38.0	78.0	14.0	54.0
Longest Dimension of Tree Islands (m)										
Range	0.05–3.90	0.05–35.00+	0.04–35.00+	0.05–26.70	0.18–2.12	0.02–20.00	0.15–5.78	0.05–16.60	0.05–35.00+	0.05–6.70
Mean	0.87	2.95	2.67	1.70	0.60	0.92	0.93	1.09	5.28	0.80
S.D.	1.16	7.88	6.98	4.80	0.63	3.05	1.47	2.76	13.10	1.39
Most Frequent Shelter Type	Riser (n = 22)	Riser (n = 13)	Riser (n = 25)	Riser (n = 17)	Riser (n = 9)	Riser (n = 24)	Riser (n = 14)	Riser (n = 20)	Vegetation (n = 3)	Riser (n = 15)

study locations, we felt that this classification served as a more meaningful description of the tree's structural form than measurements of tree height and diameter. We scanned our alpine study areas for the presence of *Ribes* spp. however, no evidence of this alternate host of blister rust was found within our belt transects or immediate surroundings. Presence of dead trees within our belt transects was also recorded.

As a result of nutcracker seed caching, whitebark pine may occur in three growth forms: a single stem, multiple stems of the same genotype (from branches becoming leaders), and as multi-genet tree clusters (Tomback and Linhart, 1990). The latter two growth forms have two or more stems that are contiguous or fused at the base; whenever these were encountered, we treated them as a single tree (e.g., Tomback et al., 2001b).

We examined each whitebark pine for presence of blister rust and severity of infection by tallying the number of cankers in three categories (Hoff, 1992): potential (symptoms such as branch swelling but no past or present sporulation), inactive (old canker that sporulated, with dead and cracked bark and dead local foliage), and active (fresh or old aecial sacs). Finally, we recorded percent "canopy kill" in discrete categories (class 1[0%], class 2 [0–5%], class 3 [5–25%], class 4 [25–50%], class 5 [50–75%], class 6 [75–95%], class 7 [95–100%]) for each whitebark pine, defined with respect to how much of the tree's crown structure potentially supporting foliage was dead. These variables are typically used during blister rust surveys in subalpine whitebark pine communities (e.g., Tomback et al., 2005).

DATA ANALYSIS

All data were tested for normality. Since the data were not normally distributed, non-parametric tests were used for data analysis; these tests are described in Kent and Coker (1994). To determine if whitebark pine is the most frequent initiator of tree islands, we used a Chi-square goodness of fit test. To compare the incidence of blister rust between sites and between single trees and islands of multiple trees, we used the nonparametric Mann Whitney U test, as well as Spearman's rank-order correlation coefficient analysis. Standard deviations are reported with means. Statistical analyses of the data were performed using SPSS v. 13.0 for Windows.

Results

ROLE OF WHITEBARK PINE IN TREE ISLAND DEVELOPMENT

A total of 266 tree islands were recorded on the belt transects, with 134 tree islands sampled at Divide Peak and 132 sampled at Lee Ridge. The tree island density at Divide Peak was higher than that at Lee Ridge: 54 per 1000 m^{-2} vs. 35 per 1000 m^{-2}, respectively. Of the combined sample, 231 (86.8%) were individual tree islands and 35 (13.2%) were multitree islands. Species richness among the tree islands ranged from 1 to 4, with *Pinus albicaulis*, *Abies lasiocarpa*, *Pinus flexilis*, *Pseudotsuga menzeiseii*, and *Picea engelmannii* present between both study sites. Length of the longest dimension of the tree islands ranged from 0.02 to 35 m ($\bar{x}$ = 1.5 ± 4.7). Terrace risers (small-scale topographic features) were the primary geomorphic feature that facilitated tree island formation for 161 or 60% of the combined tree island sample. Vegetation was the second most important facilitator of tree island formation (29% of the combined sample). Only 2 trees islands (1.2%) were not associated with any apparent shelter.

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Of the 266 tree islands, 255 included *Pinus albicaulis*. The number of whitebark pine trees per tree island ranged from 0 to 18. The majority (242/255) of whitebark pine trees that we sampled were krummholz (94.9%). Nine trees were classified as upright (3.5%) and only 4 were classified as flagged (1.6%). We measured 150 solitary whitebark pines within our transects, and 17 multitree islands out of 35 were found with whitebark pines as apparent initiators (leeward whitebark pine immediately adjacent to a windward shelter). The majority (100/150 or 66.7%) of the solitary whitebark pines and whitebark pine initiators were associated with terrace risers. A Chi-square goodness of fit test was used to determine if any species was found significantly more as an initial tree island colonizer than other species (dead trees were omitted from the analysis). At both overall ($\chi^2 = 553.94$, df = 6, $P < 0.001$) and site specific levels (Divide Peak $\chi^2 = 152.92$, df = 4, $P < 0.001$; Lee Ridge $\chi^2 = 291.18$, df = 6, $P < 0.001$), whitebark pine was a solo, initial colonizer significantly more frequently than other conifer species.

BLISTER RUST OCCURRENCE

Of the total number of whitebark pine individuals found at the two study sites combined, 33.7% ($n = 86$) of the trees had at least one potential or certain blister rust canker; 24.3% ($n = 62$) trees had at least one active or inactive canker. Individual trees exhibited a range of canker incidence from 0 to14 for total cankers (including 'potential' cankers; $n = 285$) and active and inactive cankers, excluding 'potential' cankers ($n = 226$). We found no significant difference in median total cankers per tree between Divide Peak ($n = 137$) and Lee Ridge ($n = 118$; Z = - 1.24, $P = 0.22$, Mann Whitney *U* test) or in the median number of active and inactive cankers per tree ($Z = -0.92$, $P = 0.357$, Mann Whitney *U* test).

Although the difference in canker incidence between study sites was small, variation was high in canker incidence among the sampling transects (Table 2). Transect 2 at Divide Peak was the only transect with no cankers. Canker types were assessed separately to allow for more conservative estimates of canker incidence that excluded 'potential' cankers. Number of cankers per transect was significantly correlated with the number of whitebark pine trees per transect (Spearman's $r_s = 0.71$, $P < 0.05$ [total]; $r_s = 0.71$, $P < 0.05$ [active and inactive]). Therefore, we generated a normalized canker value for each transect (Table 2).

There were 87 active and inactive cankers and 101 total cankers in multitree islands. In solitary trees, 139 cankers were classified as active and inactive cankers, with 183 total cankers. Although we found more total cankers in solitary whitebark pine, we determined that whitebark pine in multitree islands ($n = 108$) had more cankers per tree (Fig. 3) than solitary whitebark pine individuals ($n = 146$; Total cankers, $Z = -4.63$, $P < 0.001$; Active and inactive cankers, $Z = -4.57$, $P < 0.001$, Mann Whitney *U* test).

A significant correlation ($r_s = 0.36$, $P < 0.001$) existed between length of the tree island and incidence of active and inactive blister rust cankers. There was also a significant, but weak correlation ($r_s = 0.27$, $P < 0.001$) between species richness (defined as the number of conifer species that occupy a tree island) per multitree island and total number of cankers per whitebark pine. Furthermore, we recorded a total of 6 dead whitebark pine trees on 3 transects in the Divide Peak study area and 6 dead whitebark pine trees on 4 transects in the Lee Ridge study area, all with clear blister rust symptoms, indicating that blister rust is killing whitebark pine at treeline in this geographic region.

Discussion

The specific goals of this study were to investigate (1) the potential relationship between the establishment of whitebark pine and krummholz tree island formation, (2) whether blister rust is present in treeline ecotone whitebark pine, and (3) the incidence and intensity of blister rust in krummholz whitebark pine in two treeline locations on the eastern slope of the Continental Divide in northern Montana. We found that blister rust infected whitebark pine at both study sites, including solitary trees that potentially initiate tree islands, which suggests that the influence of whitebark pine as a keystone species in the alpine treeline ecotone in northern Montana may be diminishing. Consequently, the influence of whitebark pine on treeline pattern and process may be changing in this eastern Continental Divide geographic region, by increasing the mortality rate of a species that is important in facilitating tree island development.

Although, there were no significant differences in the number of cankers between the two study sites, Divide Peak, the more southern site, exhibited a higher density of tree islands, a higher density of whitebark pine, and a higher total canker incidence than Lee Ridge. Overall, including both potential and actual cankers, blister rust infected 34% of whitebark pine; including only active and inactive cankers, 25% of trees were infected. These results indicate that blister rust is prevalent within the alpine treeline ecotone of the northernmost Rocky Mountain Front in Montana, and a cause for concern despite the extremely harsh conditions.

THE ROLE OF WHITBARK PINE AND TREE ISLAND DEVELOPEMENT

The results of this study confirm the importance of whitebark pine as a tree island component in treeline communities east of the Continental Divide in northern Montana. We found that the majority (95.8%) of tree islands at our alpine treeline sites contained 1 to 18 whitebark pine trees. Whitebark pine was the apparent initiating tree species for 49% of the multitree islands. Solitary whitebark pine also represented 56% of total tree islands, each tree being the potential initiator of new tree islands. Although other conifer species were found solitarily, whitebark pine comprised 67% of the total solitary trees measured. Therefore, the incidence of blister rust and associated mortality is likely to have important implications for treeline dynamics on a landscape scale.

We also found that whitebark pine is the sole initial colonizer of tree islands significantly more often than other conifers found at treeline. This finding suggests that whitebark pine plays an extremely important role in generating the spatial pattern of tree islands at alpine treeline. Consistent with the findings of other studies, (Resler, 2004; Resler et al., 2005), whitebark pine establishes in a safe microsite in tundra. However, establishment and survival through the creation of a positive carbon balance depends heavily upon microclimate. It is in this context that favorable microsites become critical in alleviating the potential destructive climatic influences that a seedling can experience during its first few years (Holtmeier, 2003).

Whitebark pine trees that survive alpine conditions may serve as facilitators of establishment and growth of other conifers, such as spruce and fir, in their immediate lee. This facilitative function of five-needled pines was observed by others in the subalpine zone (e.g., Butler, 1986; Callaway, 1998). Over time and space the colonization and facilitation interactions have the ability to generate tree islands, and ultimately, the perpetuation of pattern on a landscape scale.

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TABLE 2

Characteristics of cankers, by transect, at Lee Ridge (LR) and Divide Peak (DR).

Study Site	Lee Ridge					Divide Peak				
Transect ID	LR1	LR2	LR3	LR4	LR5	DP1	DP2	DP3	DP4	DP5
Whitebark Pine Trees/Transect	17	25	37	29	10	42	20	35	16	24
No. Total Cankers/Transect	5	19	68	40	5	33	0	54	24	37
Normalized Canker Value*	0.29	0.76	1.79	1.48	0.50	0.79	0.00	1.54	1.50	1.54
Range per tree	0–3	0–7	0–10	0–11	0–3	0–13	—	0–10	0–8	0–14
Mean	0.29	0.76	1.83	1.38	0.40	0.79	—	1.54	1.5	1.54
S.D.	0.77	1.69	2.42	2.44	0.97	2.25	—	2.49	2.6	3.69
No. Potential Cankers/Transect	2	1	26	4	3	8	0	10	2	4
Normalized Canker Value*	0.12	0.05	0.69	0.15	0.30	0.19	0.00	0.29	0.13	0.17
Range per tree	0–1	0–1	0–8	0–3	0–3	0–2	—	0–2	0–1	0–1
Mean	0.12	0.04	0.70	0.13	0.30	0.19	—	0.29	0.13	0.17
S.D.	0.11	0.20	1.61	0.58	0.95	0.45	—	0.57	0.34	0.38
No. Inactive Cankers/Transect	3	12	24	18	1	6	0	31	8	20
Normalized Canker Value*	0.18	0.48	0.63	0.67	0.10	0.14	0.00	0.89	0.50	0.83
Range per tree	0–3	0–6	0–5	0–4	0–1	0–3	—	0–10	0–3	0–10
Mean	0.18	0.48	0.64	0.62	0.10	0.14	—	0.89	0.50	0.83
S.D.	0.52	1.36	1.29	1.04	0.31	0.57	—	2.08	1.03	2.48
No. Active Cankers/Transect	0	6	18	19	0	19	0	14	14	13
Normalized Canker Value*	0.00	0.24	0.47	0.70	0.00	0.45	0.00	0.40	0.88	0.54
Range per tree	—	0-2	0-6	0-9	—	0-11	—	0–4	0–8	0–5
Mean	—	0.24	0.48	0.66	—	0.45	—	0.40	0.88	0.54
S.D.	—	0.52	1.19	1.76	—	1.85	—	0.88	2.09	1.31
Mode, Canopy Kill Class	3 (n = 7)	2 (n = 10)	2 (n = 12)	2 (n = 12)	4 (n = 4)	2 (n = 18)	2 (n = 13)	2 (n = 14)	2 (n = 12)	2 (n = 9)

* Number of cankers/number of whitebark pine present in transect.

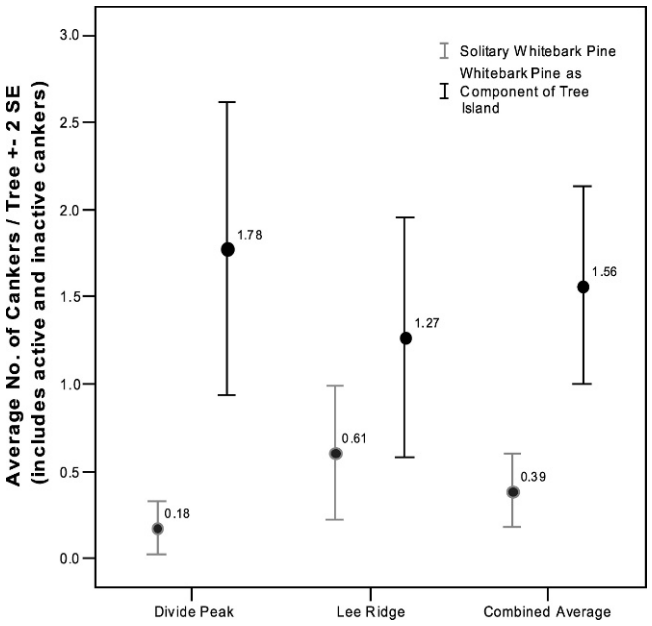


FIGURE 3. Blister rust cankers on whitebark pine trees by site and growth arrangement.

Our field observations, and the results of previous work (Resler, 2004) indicate that whitebark pine has an important role in tree island formation in this geographic region. The infection and mortality of krummholz whitebark pine from blister rust have broad implications for treeline dynamics in these and perhaps other high elevation ecosystems, as follows: The development of a tree island initially requires the dispersal of a seed to a protected microsite, followed by germination and survival of the seed. Because nutcrackers are the primary seed dispersers for whitebark pine, moving seeds from subalpine forests to treeline (e.g., Tomback, 1986), this process depends on the suitability of the seed caching microsites selected by nutcrackers for seed germination. Nutcrackers often cache seeds in microsites near objects, such as at the base of rocks, trees, or logs (e.g., Tomback, 1978; Tomback, 1998), which provide shelter against wind or shade (e.g., Mellmann-Brown, 2005). The microsites for tree island initiation must also be conducive to long-term survival of the tree (e.g., Resler et al., 2005). The hardiness of whitebark pine seedlings (e.g., Tomback et al. 2001b; Mellmann-Brown, 2005) suggests that a whitebark pine may be more likely to establish and survive in these microsites at treeline than other treeline conifer species.

We determined, in fact, that many of the locations for whitebark pine establishment were in the lee of microtopography or vegetation. The sheltering effect of vegetation or microtopography can play an important role in the amelioration of microclimates near mountain timberlines, thereby improving local site conditions of conifers (Billings and Mark, 1961; Barry, 1992; Anderson and Bliss, 1998; Körner, 1999; Smith et al. 2003). Maher et al. (2005) found that photosynthesis in whitebark pine seedlings was greater near trees and other vegetation, compared with seedlings found away from trees and herbs. The benefits include moderating temperatures, providing protection to plants from severe weather and wind, influencing soil conditions, and serving as seed traps (Marr, 1977; Carlsson and Callaghan, 1991; Nuñez et al., 1999; Parker and Sanford, 1999). Sufficient microclimatic modification by shelters may enable a seedling to live long enough for it to begin modification of its own environment through positive feedback mechanisms (Resler et al., 2005).

IMPLICATIONS OF BLISTER RUST

The presence of blister rust at treeline in this geographic region has the potential to disrupt the dynamics of tree island formation. We determined that established, solitary whitebark pine trees initiate tree islands in the majority of cases, providing sheltered microsites for less hardy species. Blister rust, however, is reducing the vigor of whitebark pine, ultimately killing small trees within a few years (e.g., Tomback et al., 1995), and therefore potentially limiting the sites conducive to tree island establishment. Thus, with blister rust infecting treeline whitebark pine east of the Continental Divide, the timeframe, dynamics, and conditions for tree island development may change, with fewer tree islands initiated over time. This situation may be further exacerbated by a decline in whitebark pine seed production, and thus the reduced dispersal of seeds to treeline, as whitebark pine trees in the subalpine forest below continue to succumb to blister rust. Past assessments of subalpine zone whitebark pine in the same geographic region indicate blister rust infection levels of around 80% or greater (Kendall and Keane, 2001), with canopy kill and tree death diminishing seed production greatly.

Treeline vegetation dynamics may also change with trends in climate warming. Changes in the elevation of treelines have been associated with variation in regional climate since the last glacial maximum (Rochefort et al., 1994; Lloyd and Graumlich, 1997). Nutcrackers generally facilitate the upward movement of whitebark pine by seed caching in tundra microsites as well as within the treeline ecotone (e.g., Tomback, 1986; Tomback, 1998 and references within; Tomback, 2001). Thus, because of whitebark pine's role as a facilitator, it follows that krummholz tree islands should develop at higher elevations. Initial establishment and survival of conifers in favorable sites at locations higher in elevation than established trees, are important first steps in treeline migration in response to climate change (Butler et al., 2004; Resler et al., 2005). However, with the spread and intensification of white pine blister rust, these events may not be realized.

BLISTER RUST AND LANDSCAPE PATHOLOGY

The relatively new field of landscape pathology recognizes that both the spread of pathogens and disease expression are influenced by landscape structure, configuration, and size of landscape components (Holdenrieder et al., 2004). We compared the incidence of blister rust incidence in solitary trees to blister rust incidence in tree islands with more than one conifer. The incidence of blister rust was significantly higher in tree islands with multiple trees for the combined sample. We also found a significant correlation between length of the tree island and incidence of active blister rust cankers, indicating that patch size is an important landscape metric in incidence of blister rust at our study sites. The difference in blister rust incidence between solitary trees and trees in multitree tree islands warrants investigation into underlying mechanisms, such as the difference in microclimate and spore survival in tree islands vs. solitary trees. Also, more research on the relationships between landscape pattern and function is needed to understand fully the correlation between patch size and blister rust infection incidence. However, given that *Cronartium ribicola* spores are wind dispersed, it is possible that larger tree islands, simply by having a larger surface area (and resulting differences in boundary conditions) have a higher chance of being infected than smaller, individual trees. It is also possible that large tree islands maintain higher humidity or buffer microclimate conditions, permitting spore survival. Patch size, and tree island category may also help to explain the high variability of blister

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rust incidence among transects within study sites. Ironically, the same conditions that mitigate environmental stress for tree establishment and growth may foster infection of whitebark pine by blister rust.

Our ability to confidently extrapolate the results of this study to other treeline locations is limited at this time, given the small geographic study area in which we worked. However, given that high blister rust infection levels have been found to the south, north, and west of our study sites in the northern Rocky Mountains (Kendall and Keane, 2001; Smith et al., 2008), we would expect to find blister rust infecting whitebark pine elsewhere in the region. Climate on the west side of the Continental Divide may be less extreme, and it is possible that other vegetation dynamics exist, such that tree island establishment does not depend on initial whitebark pine presence in sheltered microsites. The dynamics of tree island establishment west of the Continental Divide and even farther south along the Rocky Mountain Front, where regional climate may differ, warrants further study.

LOSING WHITEBARK AS A FOUNDATION SPECIES IN THE ALPINE TREELINE ECOTONE

The exotic fungal pathogen, white pine blister rust, threatens the continued occurrence of whitebark pine in the alpine treeline ecotone in two ways: First, as trees in the subalpine forest zone succumb to blister rust, they lose their ability to produce seeds (e.g., Hoff et al., 2001). Consequently, fewer seeds are available for nutcrackers to disperse to the alpine treeline ecotone (e.g., Tomback, 1986). Second, apparently blister rust is killing the trees that have become established in the ecotone, and many may succumb before they facilitate the recruitment of other conifers. With the diminished presence of whitebark pine, the dynamics of treeline establishment will be disrupted, potentially resulting in altered community structure in this region of the northern Rocky Mountains. Loss of whitebark pine may alter ecosystem services, such as avalanche control and local hydrology, and even alter potential ecosystem responses to climate change.

The widespread decline of whitebark and other western five-needled white pines as a result of blister rust argues for the design and implementation of coherent management plans. Healthy whitebark pine trees in areas with high incidence of blister rust are being screened for genetic resistance (e.g., Mahalovich and Dickerson, 2004; Schwandt, 2006). These trees are being used as the basis of restoration programs. In addition to planting seedlings grown from blister rust resistant parent trees in the subalpine zone, managers should consider planting resistant seedlings in the treeline ecotone in sheltered microsites where natural whitebark pine seedlings have succumbed to blister rust. In the meantime, with the ongoing losses of whitebark pine communities, western biodiversity and many ecosystem services are on the decline.

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