White Pine Blister Rust Severity and Selection of Individual Whitebark Pine by the Mountain Pine Beetle (Coleoptera: Curculionidae, Scolytinae)[1]

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Abstract We investigated whether white pine blister rust (*Cronartium ribicola*) (J.C. Fischer in Rabenh.) severity, tree diameter at breast height (DBH), bark and phloem thickness, and sapwood moisture content influence the preference of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) for individual trees of whitebark (*Pinus albicaulis* Engelm.) and lodgepole pine (*P. contorta* Loud.). We measured these variables at 5 sites in Montana and Idaho and found a significant relationship between blister rust severity and attack of trees by *D. ponderosae*, with trees exhibiting greater blister rust severity being more likely to be attacked by the beetle. Sapwood moisture content was negatively correlated ($P = 0.0004$) with blister rust severity indicating that as severity increases there is an increasingly negative effect on water relations within the tree. Sapwood moisture content was significantly lower in *P. albicaulis* than in *P. contorta* at sites with beetle activity suggesting that there may be an interaction between blister rust severity and drought stress that, in turn, may affect beetle preference. DBH and bark and phloem thickness did not appear to influence beetle preference for individual trees. As blister rust spreads in *P. albicaulis* stands across the western U.S., this may translate to increasing levels of beetle-caused mortality in these areas.

Key Words *Dendroctonus ponderosae, Cronartium ribicola, Pinus albicaulis,* bark beetle

Whitebark pine (*Pinus albicaulis* Engelm.) is a five-needle pine that dominates many western North American subalpine forests. While *P. albicaulis* is rarely a commercially exploited timber species, it has considerable ecological, cultural, and recreational value (Lanner 1996, Tomback et al. 2001). It is considered a keystone species. In the high elevation zones where it occurs, its loss would result in a permanent lowering of the treeline, negative impacts on snow retention and hydrological processes, and the loss or significant reduction of many plant and animal species (Arno and Hoff 1989).

Unfortunately, *P. albicaulis* is in rapid decline across much of its range (Keane and Arno 1993) with some areas already experiencing as much as 90% mortality. This decline is due to 3 factors, the most important being white pine blister rust (*Cronartium ribicola* [J.C. Fischer in Rabenh.]), an exotic disease to which *P. albicaulis* is highly

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susceptible (Hoff et al. 1980, McDonald and Hoff 2001). Another important factor is the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), an aggressive indigenous insect that kills only scattered trees during endemic periods, but can cause high levels or even complete mortality of mature *P. albicaulis* over large areas during outbreaks (Ciesla and Furniss 1975, Bartos and Gibson 1990). *Dendroctonus ponderosae* prefers the large, mature cone-bearing trees upon which regeneration is dependent. Where considerable loss of large numbers of *P. albicaulis* due to *C. ribicola* occur, *D. ponderosae* accelerates the stand decline directly by killing mature trees and indirectly through its impact on reproduction. Finally, fire suppression has allowed the encroachment of shade-tolerant trees, primarily the subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), into many stands of shade-intolerant *P. albicaulis* (Arno 1986, Murray et al. 1998, Morgan and Murray 2001) contributing further to its decline. Stands choked with *A. lasiocarpa* provide few suitable sites for germination of *P. albicaulis* pine seeds, growth of seedlings, or for seed caching by Clark's nutcrackers (*Nucifraga columbiana* Wilson), the primary agents of dispersal of *P. albicaulis* (Hutchins and Lanner 1982, Tomback 2001).

Little is known about the dynamics and interactions of insects and pathogens associated with *P. albicaulis* (Bartos and Gibson 1990). This lack of information has greatly hampered management and restoration efforts. Most restoration efforts to date have focused on increasing regeneration and developing resistance to *C. ribicola* (Keane and Arno 2001, Waring and Six 2005). Little attention has been focused on the study of *D. ponderosae* population dynamics and phenology in *P. albicaulis* or this insect's interaction with pathogens such as *C. ribicola*. However, due to the development of extensive outbreaks of *D. ponderosae* in *P. albicaulis* in recent years (Logan and Powell 2001, Meyer 2005), and the consequent loss of a significant proportion of the few remaining mature *P. albicaulis* at many sites, interest in the biology of this insect in high elevation ecosystems is now increasing.

In 2000 and 2001, while conducting surveys of white pine blister rust in *P. albicaulis*, we observed considerable activity of *D. ponderosae* in *P. albicaulis* in several mixed stands containing both *P. albicaulis* and *P. contorta* Loud. However, in these same stands, we saw little-to-no concurrent beetle activity in *P. contorta*. The high variability in blister rust infection severity among individual trees that we observed, and the fact that *P. contorta*, for the most part, remained unattacked by the beetles, led us to speculate as to what factors may be driving beetle preference for particular individual *P. albicaulis*, and for *P. albicaulis* over *P. contorta*, at these sites. It is well known that stress, which can be caused by a number of factors including drought and disease, can reduce constitutive and inducible defenses in pines, thereby lowering their resistance to attack by bark beetles (Cates and Alexander 1982, Waring and Pitman 1985, Lorio 1993). If *C. ribicola* (which does not attack *P. contorta*) causes stress in infected *P. albicaulis*, it may potentially increase susceptibility of these trees to beetle attack.

Factors other than blister rust may also influence beetle preference for individual trees and species of trees. *Pinus albicaulis* may be preferred by the beetle if it is a superior food source (e.g., possesses thicker or more nutritious phloem). Conversely, higher susceptibility may be due to an inferior innate defensive system in *P. albicaulis* relative to that of *P. contorta* or to greater levels of stress in *P. albicaulis* than in *P. contorta* in these stands. Greater stress in *P. albicaulis* could stem from *C. ribicola* infection or from a more rapid and acute response by this tree to drought.

Our primary objective with this study was to investigate the factors that may influence the preference of *D. ponderosae* for individual *P. albicaulis* and whether differences in host tree characteristics may account for the strong preference of *D. ponderosae* for *P. albicaulis* over *P. contorta* that we observed. Primarily, we wished to determine whether white pine blister rust severity in *P. albicaulis* affects beetle preference. If infection by *C. ribicola* creates stress in trees, and consequently increases susceptibility of trees to beetles, we should observe an increase in preference as severity of disease increases. Secondly, we wanted to compare sapwood moisture content in *P. contorta* and *P. albicaulis.* Sapwood moisture content can be used to estimate the degree of hydration of a tree relative to other trees in the same stand and may be useful as a coarse indicator of stress. Lastly, we wanted to compare characteristics of *P. albicaulis* and *P. contorta* that may affect beetle preference, and reproductive and developmental success, including tree diameter and bark and phloem thickness.

Materials and Methods

Study sites. Site locations and characteristics are summarized in Table 1. All sites consisted of mixed stands of *P. albicaulis, P. contorta*, and *A. lasiocarpa.* Beetles were active at four of the five sites (Table 1). Trees in stands at all sites were mostly even-aged, a condition typical of high elevation forests in western North America, given that they often regenerate after stand-replacement fire.

Disease ratings and tree characteristics. At the 4 sites where *D. ponderosae* was active (Point Six, Nut Basin, Beaver Ridge, and Boulder Creek), we rated *C. ribicola* severity in both *D. ponderosae*-attacked and unattacked *P. albicaulis.* Ratings of trees were conducted at Point Six and Beaver Ridge in 2001 and 2002, at Nut Basin in 2002, and at Boulder Creek in 2003 (Table 1). In early-to-mid summer at each site, we located 20 *P. albicaulis* trees that had been attacked by *D. ponderosae* the previous summer but whose foliage had not yet turned yellow or red (foliage typically turns color in mid to late summer the year after attack). Because foliage of these trees was still green, flagging (dead foliage and branches) due to blister rust was easily discernable in the crown allowing the accurate rating of *C. ribicola* infection

Table 1. Location of sites used to assess preference of *D. ponderosae* for individual whitebark and lodgepole pine

Site	Beetles	Location	Elevation (m)	Years sampled
Point Six	Yes	Lolo National Forest, Missoula, MT	2414	2001, 2002
Beaver Ridge	Yes	Clearwater National Forest, ID	2246	2001, 2002
Nut Basin	Yes	Nez Perce National Forest, ID	2268	2002
Bear Overlook	No	Bitterroot National Forest, MT	2140	2002
Boulder Creek	Yes	Flathead Indian Reservation, MT	2298	2003

severity. For each of these trees we measured diameter at breast height (DBH) (approx. 1.4 m above the soil line) and rated them for blister rust severity using the rating system developed by Six and Newcomb (2006). Briefly, the rating system divides both the crown and the bole of the tree into thirds and rates each third separately for percent area of tree visibly affected by the disease. Crown and bole ratings are then added for a total severity rating for the tree. The potential range of total tree scores that are possible with the system are 0 (no infection) to 18 (completely infected). In reality, total infection scores above 14 (the highest we have ever assigned a tree) are unlikely and few trees survive infection levels resulting in a score of 12 or higher. The 3 nearest neighboring unattacked *P. albicaulis* (>17 cm DBH) to each of the 20 trees attacked by *D. ponderosae* were then located, measured for DBH, and rated for blister rust severity. This sampling scheme allowed comparisons of blister rust severities of attacked trees with those of unattacked trees. Unequal sample sizes among sites resulted from either our inability to locate 20 attacked trees at sites with low recent beetle activity, or an inability to locate 3 unattacked nearest neighbor trees for each attacked tree (particularly difficult when attacks were clumped). Additional sampling was conducted when attacked trees were abundant and time allowed. Trees with visible signs of mistletoe infection were not used (Beaver Ridge and Boulder Creek).

For each unattacked *P. albicaulis* we also measured bark and phloem thickness and sapwood moisture content. On the north and south side of each tree at 1.4 m, bark and phloem thicknesses were estimated by cutting into the bark to the sapwood, removing a small rectangle of the bark, inserting a ruler, and measuring outer bark (dead layer) and phloem (living layer) to the nearest 0.5 mm. The north and south side measurements were then combined and averaged for each tree. We inserted the probes of a Protimeter™ (Protimeter PLC, Marlow, UK) to measure sapwood moisture content into the exposed sapwood where bark was removed for bark and phloem measurements. Protimeters are useful for making coarse estimations of moisture content in wood displaying between 5-65% moisture content. For trees whose sapwood moisture contents were <65%, the actual Protimeter reading was recorded. For readings ≥65%, we recorded 65%. Protimeter readings from the north and south sides of trees were combined and averaged for each tree.

During assessments of *P. albicaulis* at each site, a number of randomly-located unattacked *P. contorta* (>17 cm DBH) that were interspersed with the attacked and unattacked *P. albicaulis* were also located and measured for DBH, bark and phloem thickness, and sapwood moisture content. At Boulder Creek, both *P. albicaulis* and *P. contorta* were attacked by *D. ponderosae*. At this site we also measured DBH of all *P. contorta* we found that were attacked the prior year (2002). Although our sampling at Boulder Creek was conducted in 2003, we were also able to locate several *P. contorta* and *P. albicaulis* that had been attacked in 2001 and measured the DBH of these trees as well.

Data analyses. Differences between blister rust severity ratings and between DBH of attacked and unattacked *P. albicaulis* for each year within a site were assessed using Student's *t*-tests. Student's *t* was also used to detect differences within sites for DBH, bark and phloem thickness, and sapwood moisture content of unattacked *P. contorta* and unattacked *P. albicaulis*, and between DBH of *D. ponderosae*-attacked *P. albicaulis* and *D. ponderosae*-attacked *P. contorta* at Boulder Creek. The relationship between beetle attack and blister rust severity rating was assessed using logistic regression with severity rating designated as the independent variable and *D.*

ponderosae-attack/no attack as the dependant variable. The relationship between sapwood moisture content and blister rust severity was assessed using Pearson Product Moment Correlation analyses. All statistics were conducted using SigmaStat version 2.03 (SPSS 1997).

Results

Mean blister rust severity ratings ranged from 3.03-10.42 among sites with *D. ponderosae* activity (Table 2). Mean blister rust severity was 6.33 (SE 1.06) for the Bear Overlook site, which had no beetle activity. For within-site comparisons, there was a trend for severity ratings to be higher in *D. ponderosae*-attacked trees than in unattacked trees at all sites in all years, although within-site differences were significant only at Beaver Ridge in 2001 and 2002, and at Point Six in 2001 (Table 2). However, logistic regression including data for all *P. albicaulis* sampled across all years and all sites (excluding Bear Overlook which had no beetle activity) found a highly significant relationship between blister rust severity and beetle attack ($n = 232$, Wald statistic: 22.455, $P < 0.001$).

DBH was significantly different between attacked and unattacked *P. albicaulis* only at Beaver Ridge in 2001. There was no consistent trend for attacked trees to be larger or smaller than unattacked trees (Table 2). There was also no significant difference in DBH of *P. albicaulis* and DBH of *P. contorta* attacked by *D. ponderosae* at Boulder Creek in 2001 or 2002 (df = 45, t = –0.697, $P = 0.490$ for 2001; df = 21, t = 1.963, $P = 0.063$ for 2002).

Comparisons of characteristics of unattacked *P. albicaulis* and unattacked *P. contorta* at each site showed a slight trend for *P. contorta* to be larger than *P. albicaulis*, but the difference was significant only at Nut Basin (Table 3). There was no trend for

Table 2. Mean (SE) *C. ribicola* severity ratings (RR) and DBH of whitebark pine attacked and not attacked by *D. ponderosae* at four sites in Montana and Idaho. (Bold values indicate significant differences between values of attacked and unattacked trees within years at a site. Levels of significance = *0.01, **0.001)

Site	Year sampled	Beetle-killed	N	RR	DBH (cm)
Point Six	2001	No	60	**6.27 (0.34)****	27.69 (0.86)
	2001	Yes	35	**9.35 (0.38)**	28.03 (1.10)
	2002	No	71	5.00 (0.37)	27.74 (0.76)
	2002	Yes	20	6.55 (0.85)	29.62 (2.69)
Beaver Ridge	2001	No	63	**6.33 (0.35)****	**31.50 (0.89)***
	2001	Yes	31	**10.42 (0.38)**	**35.38 (1.23)**
	2002	No	43	**5.41 (0.50)****	30.84 (1.22)
	2002	Yes	12	**9.09 (0.56)**	29.00 (1.83)
Nut Basin	2002	No	20	3.03 (0.57)	31.88 (1.42)
	2002	Yes	10	3.40 (0.87)	36.45 (3.18)
Boulder Creek	2003	No	14	3.71 (1.13)	29.40 (1.51)
	2003	Yes	12	4.10 (1.08)	28.00 (1.85)

Table 3. Mean (SE) DBH, bark and phloem thickness, and sapwood moisture content, for whitebark and lodgepole pine not attacked by *D. ponderosae* at five sites in Montana and Idaho. (Bold values indicate significant differences between values for *P. albicaulis* and *P. contorta* within years at a site. Levels of significance = *0.05, **0.01, ***0.001)

Site	Year	Tree species	N	DBH (cm)	Bark thickness (mm)	Phloem thickness (mm)	Wood moisture content (%)
Point Six	2002	*P. albicaulis*	71	**27.74 (0.76)*** **	2.98 (0.18)	2.53 (0.10)	**61.73 (0.68)* **
	2002	*P. contorta*	19	**31.04 (0.79)**	2.89 (0.27)	2.37 (0.16)	**65 (0)**
Beaver Ridge	2001	*P. albicaulis*	63	31.50 (0.89)	**2.97 (0.13)* **	**4.17 (0.16)*** **	**36.10 (0.79)*** **
	2001	*P. contorta*	30	32.72 (1.91)	**3.61 (0.17)**	**1.89 (0.09)**	**52.02 (1.21)**
	2002	*P. albicaulis*	43	30.84 (1.22)	3.23 (0.19)	3.01 (0.17)	**59.41 (0.97)* **
	2002	*P. contorta*	20	35.41 (2.44)	2.82 (0.23)	3.16 (0.27)	**64.47 (0.53)**
Nut Basin	2002	*P. albicaulis*	20	**31.88 (1.42)*** **	**2.82 (0.21)*** **	**3.17 (0.23)* **	**58.47 (1.90)** **
	2002	*P. contorta*	20	**39.80 (1.91)**	**4.25 (0.30)**	**2.40 (0.21)**	**64.15 (0.85)**
Bear Overlook	2002	*P. albicaulis*	12	28.94 (1.23)	**2.21 (0.26)** **	**2.00 (0.15)* **	63.33 (1.12)
	2002	*P. contorta*	21	27.10 (0.69)	**1.17 (0.16)**	**1.14 (0.14)**	62.76 (1.07)
Boulder Creek	2003	*P. albicaulis*	14	29.40 (1.51)	4.89 (0.54)	5.89 (0.47)	**52.57 (2.25)** **
	2003	*P. contorta*	10	31.42 (2.06)	5.60 (0.60)	5.70 (0.54)	**62.00 (1.53)**

bark thickness to be greater in one species of tree than the other. At Nut Basin, bark of *P. contorta* was significantly thicker than that of *P. albicaulis*, whereas at Bear Overlook, bark was significantly thicker in *P. albicaulis*. Bark thickness was not significantly different between the 2 tree species at any other site. Phloem tended to be thicker in *P. albicaulis* than *P. contorta*, but significantly so only at Beaver Ridge in 2001, Nut Basin, and Bear Overlook (Table 3).

Sapwood moisture content was lower in *P. albicaulis* than *P. contorta* at all sites, and significantly so for all sites and years except for Bear Overlook, where both tree species had similar, relatively high, moisture contents (Table 3). Sapwood moisture content was negatively correlated with blister rust severity rating ($r = -0.253$, $n = 195$, $P = 0.0004$).

Discussion

Our results indicate that the selection of individual *P. albicaulis* by *D. ponderosae* may be influenced by white pine blister rust severity, with trees exhibiting greater severity being more likely to be attacked by the beetle. In addition, sapwood moisture content was negatively correlated with blister rust severity rating indicating that as infection severity increases there is an increasingly negative effect by the fungus on water relations within the tree. Whereas the mechanism underlying the reduction in sapwood moisture in trees infected by *C. ribicola* is unknown, lower moisture in the sapwood may create, or be a manifestation of, stress in infected trees, which may subsequently result in lower defenses against beetles.

Our results suggest that while blister rust severity influences beetle preference for individual trees, it may not, by itself, be an initiating factor of beetle activity at a site. For example, the site with no beetle activity, Bear Overlook, had an average infection severity rating of 6.33 in *P. albicaulis*, much higher than mean infection severity ratings for trees at Nut Basin and Boulder Creek where beetles were active. More likely, a trigger creating stress, such as drought, may elicit the initial response of beetles to a stand, after which differences in tree susceptibility likely determine the distribution of beetle attacks. Our study was conducted during a drought which may have influenced the patterns of beetle activity we observed at our sites. Trees of both species at Bear Overlook (a wet site relative to the others and with no beetle activity), exhibited equivalent, and relatively high, sapwood moisture contents. However, in all other stands that we sampled, all of which exhibited beetle activity, sapwood moisture content was significantly lower in *P. albicaulis* than in *P. contorta*. This suggests that there may be an interaction between blister rust severity and drought stress that increases susceptibility in some *P. albicaulis* more than in others, and in *P. albicaulis* earlier than in *P. contorta*.

In combination with the effects of recent warming trends associated with climate change on beetle phenology and survival at high elevation sites (Logan and Powell 2001), white pine blister rust, through its effects on tree physiological processes, may be increasing the proportion of susceptible trees in *P. albicaulis* stands just at the time that warm temperatures are supporting increased levels of beetle activity. The results of this study indicate a considerable need to focus research efforts on interactions among *C. ribicola*, tree defenses, *D. ponderosae*, and the environment.

In summary, white pine blister rust severity appears to influence preference of *D. ponderosae* for individual *P. albicaulis*. This has serious implications for the preservation of this keystone species in high elevation ecosystems and the many species that are dependent upon this tree including the endangered grizzly bear (Kendall 1983, Mattson et al. 2001). In our study, as blister rust severity increased, trees displayed increasing levels of beetle attack. As blister rust continues to spread in *P. albicaulis* stands across the west, this may translate to increasing levels of beetle-caused mortality with a continual decrease in habitat quality and ecosystem function at affected sites.

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