The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado

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Abstract: A survey of limber pine (*Pinus flexilis* James) to determine the geographic distribution, incidence, and severity of white pine blister rust (WPBR) throughout 13 study areas in central and southeastern Wyoming and northern Colorado was conducted from 2002 to 2004. The majority (81.1%) of the 18 719 surveyed limber pines >1.37 m tall were classified as healthy, 13.5% were declining or dying from various causes, and 5.4% were dead. WPBR was present on 278 (55%) of the 504 survey plots. Incidence of the disease ranged from 0% to 100% and averaged 15.5% over all the plots and 28.0% on the infested plots. Likelihood of infection by WPBR was significantly greater for limber pines in larger diameter classes. Incidence was negatively correlated with elevation and positively correlated with geographic position, with more northerly and easterly plots having higher incidences of WPBR. Incidence varied by slope position and did not vary by aspect, slope configuration, or degree of canopy closure. The current level of infestation in central and southeastern Wyoming and northern Colorado has been attained within the past two to four decades. With time, the pathogen may spread to currently uninfested white pine populations and intensify throughout its current distribution impacting valuable ecosystems.

Résumé : Un inventaire du pin flexible (*Pinus flexilis* James) a été réalisé de 2002 à 2004 dans 13 zones d'étude situées dans le centre et le sud-est du Wyoming et le nord du Colorado pour déterminer la répartition géographique, l'incidence et la sévérité de la rouille vésiculeuse du pin blanc (RVPB). La majorité (81,1 %) des 18 719 pins flexibles échantillonnés de plus de 1,37 m de haut ont été classés comme sains, 13,5 % dépérissaient ou étaient mourants sous l'effet de diverses causes et 5,4 % étaient morts. La RVPB était présente dans 278 (55 %) des 504 places-échantillons. L'incidence de la maladie variait de 0 % à 100 % et atteignait en moyenne 15,5 % dans l'ensemble des places-échantillons et 28,0 % dans les places-échantillons infectées. Les risques d'infection par la RVPB étaient significativement plus élevés pour les pins flexibles dans les classes de diamètre supérieures. L'incidence était négativement corrélée avec l'altitude et positivement corrélée avec la position géographique : les places-échantillons les plus au nord et les plus à l'est avaient les plus fortes incidences de RVPB. L'incidence variait selon la position de la pente mais non selon l'exposition, la configuration de la pente ou le degré de fermeture du couvert. Le niveau actuel d'infection dans le centre et le sud-est du Wyoming et le nord du Colorado a été atteint au cours des deux à quatre dernières décennies. Avec le temps, le pathogène pourrait progresser vers les populations de pin blanc non infectées et l'infection pourrait s'intensifier partout où la maladie est actuellement présente et affecter des écosystèmes de grande valeur.

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Introduction

Cronartium ribicola (J.C. Fischer ex Rabh.), the causal agent of white pine blister rust (WPBR), is native to Eurasia and was widespread and well established in Europe by the beginning of the 20th century (Mielke 1943; Hunt 2003). In 1910, this forest pathogen was introduced to western North America via infected nursery stock imported from France to Point Grey near Vancouver, British Columbia (Mielke 1943). *Cronartium ribicola* is a heteroecious rust capable of infecting all North American white pines (members of subgenus *Strobus* (Haploxylon or soft pines), section *Strobus*, subsections *Strobi* and *Cembrae* and section *Parrya*, subsection *Balfourianae* (Price et al. 1998)) as primary hosts. Species in the genus *Ribes* (Grossulariaceae), currants and gooseberries, are the alternate hosts required by the pathogen to complete its life cycle. Recent evidence from northern Idaho indicates that the fungus is also capable of using forbs in the family Orobanchaceae as alternate hosts, but this appears to be a rare occurrence (McDonald et al. 2006). Primary infection of the pine host occurs on needles, after which the fungus grows into the bark of branches and stems, where potentially girdling cankers are produced (Lachmund 1933; McDonald and Hoff 2001). Long-distance spread of the pathogen occurs through aeciospores produced on the pine host, which are capable of traveling on wind currents up to several hundred kilometres to infect a susceptible alternate host (Mielke 1943).

After infection by WPBR, mature white pines are able to survive for several years; however, they typically experience declines in cone production resulting from the killing of upper branches, on which nearly all cones are produced

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(McCaughey 1994). WPBR also acts to prevent regeneration of white pines by readily infecting and killing seedlings and saplings (Mielke 1943). Estimates of WPBR-caused mortality at levels greater than 90% have been reported in northern Idaho and western Montana (Hagle et al. 1989; Kendall and Arno 1990,).

The susceptible white pines in Colorado and Wyoming are whitebark pine (*Pinus albicaulis* Engelm.*)*, limber pine (*Pinus flexilis* James), Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.), and southwestern white pine (*Pinus strobiformis* Engelm.). Limber pine, the focus of this study, grows across a vast latitudinal range (34°–54°N) on sites that range in elevation from 870 m to approximately 3810 m (Steele 1990). Between 40° and 45°N, the area encompassing this study, limber pine can be a major component of stands along both the upper and lower tree lines. Limber pine is considered relatively shade intolerant and, thus, seral to many of the species with which it cooccurs, but it will codominate with aspen (*Populus tremuloides* Michx.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies bifolia* A. Murr.) and Rocky Mountain bristlecone pine (Peet 1981; Steele 1990). Although limber pines have limited value as timber species, they provide erosion protection in watersheds; increase snowpack; provide cover and a nutritious food source for wildlife including birds, rodents, and bears (Steele 1990; Walker 1999); and increase esthetic values and recreational opportunities. Limber pine also often acts as a pioneer species following disturbances such as fire and avalanches (Steele 1990).

Following its introduction to western North America, the WPBR pathogen spread through native white pine populations. Periodic examinations of whitebark, limber and Rocky Mountain bristlecone pines and their associated *Ribes* species in Wyoming and Colorado since 1934 indicate that the pathogen is spreading to the south and east (USDA Forest Service 1950, 1951, 1952, 1959; Brown 1967, Brown 1978, Benedict 1981). WPBR was first reported in Colorado in 1998 on the Roosevelt National Forest along the Wyoming border (Johnson and Jacobi 2000). In 2003, isolated WPBR infestations were discovered on both limber and RM bristlecone pines in the Wet and Sangre de Cristo Mountains of southern Colorado, more than 450 km from other known infections (Blodgett and Sullivan 2004).

Although limber pine is an important component of many forested ecosystems in Wyoming and Colorado, very little is known about the distribution of white pine blister rust and its impacts on limber pines. The objectives of this study were to (*i*) determine the geographic distribution, incidence, and severity of WPBR throughout central and southeastern Wyoming and northern Colorado and (*ii*) determine if incidence of WPBR varies in relation to site variables and tree characteristics.

Methods

Study areas

Surveys occurred on 13 study areas defined by government management units and geographic features in Wyoming and Colorado, including Bureau of Land Management lands; the Medicine Bow, Roosevelt, and Shoshone National Forests; and the Wind River Indian Reservation (Fig. 1). These study areas were selected to encompass areas in Wyoming where the pathogen has been for 5–40 years (USDA Forest Service 1950; Brown 1967; Johnson and Jacobi 2000) and areas with known limber pine populations but no reports of white pine blister rust.

Plot location

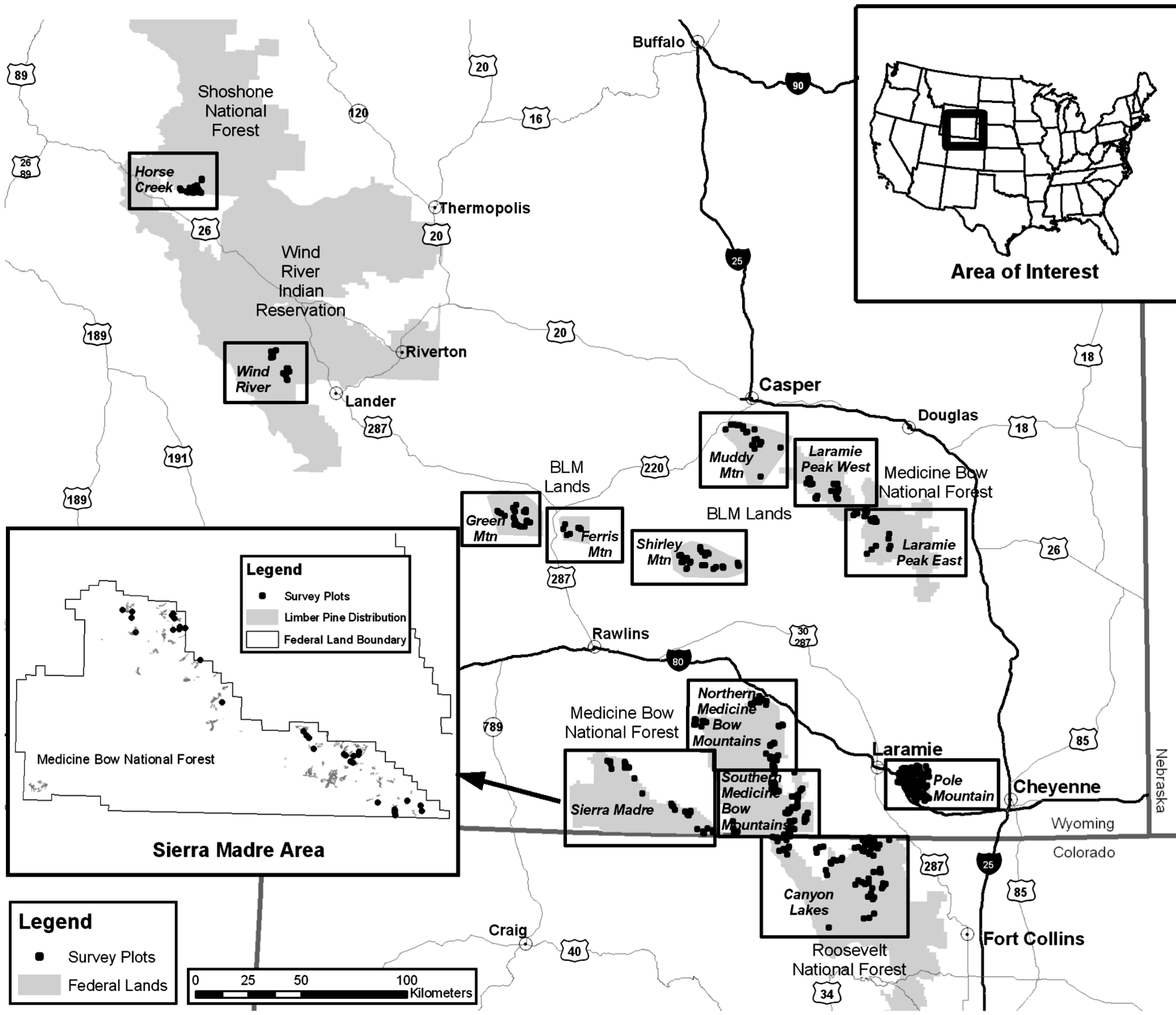
Stand-level data on the occurrence of limber pine in the Roosevelt and Medicine Bow National Forests were obtained from the USDA Forest Service Rocky Mountain Resource Inventory System database. Poststratification was employed based on site characteristics in an attempt to capture the variability of site conditions under which limber pine grows and ignoring WPBR conditions. Surveyed stands provided a good representation of the elevational range of limber pine and were located on all aspects, topographic positions, and forest composition types available for sampling. Plots were not established in stands where no living limber pine were present. Surveyed stands were within 3 km of a road to limit travel time between stands and maximize the number of plots established. Surveys in areas not managed by the Forest Service were directed to locations recommended by employees familiar with the areas as having significant populations of limber pine, again ignoring WPBR conditions. The series of plots established defined the study area. The Pole Mountain study area was intensively sampled for potential future spatial analysis of both large and small scale variability in WPBR occurrence.

Survey methods

Limber pine stands were sampled by belt transects using methods modified from Smith and Hoffman (2000). Two to five pine transects were located in each plot with the goal of examining at least 30 limber pine in each series of transects. If 30 limber pine were not observed after establishing five transects, no more transects were established. Pine transects were 61 m × 4.6 m and were located along random bearings through the stand. The GPS coordinates of the starting point of each transect were recorded. At the end of each pine transect, a *Ribes* transect (30.5 m × 4.6 m) was established along the same bearing, in which the *Ribes* species present, total number of stems or bushes, mean number of stems per bush, mean stem length, and the presence of *C. ribicola* were recorded. From these data, densities of *Ribes* by species in linear metres of live stem per hectare were calculated. Subsequent pine transects were started at the end of the *Ribes* transect along another random bearing. If the random bearing required resampling of the same trees, another random bearing was selected. The series of pine and *Ribes* transects established in an area defined the plot. At each plot, elevation, slope percent, aspect, slope position, slope configuration, stand structure, dominant tree and understory cover, and disturbance history were also recorded. Using these methods, 504 plots were established in 2002–2004.

Within each pine transect the following data were recorded for all limber pines: diameter class (≤5 cm, 5.1–15.2 cm, 15.3–30.5 cm, >30.5 cm diameter at breast height

Fig. 1. White pine blister rust study areas in Wyoming and northern Colorado.



(DBH, 1.37 m)); health status (healthy, less than 5% damage to crown or stem; declining, 6%–50% of crown showing symptoms that indicates it is dead or will be; dying, >50% crown showing symptoms; recently dead, some red needles and fine twigs present; old dead, no fine twigs or needles present) regardless of cause; crown class (open, dominant, codominant, intermediate, overtopped or understory); percent live crown, number of WPBR branch and stem cankers; dwarf mistletoe rating (DMR) (Hawksworth 1977); and the type and severity of any other damage affecting 5% or more of the tree.

Trees growing in clumps were considered individual stems if they were distinct at 1.37 m height. Because of a combination of caching behavior by seed dispersers and either terminal damage or a genetic predisposition for early branching, limber pine can be found growing as tree clusters and as multiple-trunk trees in addition to the most prevalent form of single-trunk tree. Only genetic analysis can distinguish between the morphologically similar multiple-trunk trees and tree clusters. Several studies have found that the proportion of single stems ranges from 65% to 80% over the elevation range covered by this study (Lanner and Vander Wall 1980; Schuster and Mitton 1991; Carsey and Tomback 1994; Feldman et al. 1999). The composition of tree clumps is highly variable ranging from 18% (Schuster and Mitton 1991) to 81% (Carsey and Tomback 1994) composed of genetic individuals (tree clusters).

Binoculars were used to examine the crowns of trees for cankers and other damage. Two observers examined each tree, and crews alternated each week to reduce observer differences and keep crews trained as new issues arose throughout the field season. WPBR cankers were distinguished by the presence of a combination of sporulation, swelling, discoloration, rodent chewing, and evidence of past blistering. Cankers were considered stem cankers when they were on the main stem or branch cankers within 15 cm of the bole on living branches; in addition, to be considered a stem canker, the canker must have been present on a section of the stem that if girdled would remove more than 25% of the crown. Trees that were classified as old dead were not evaluated for cankers, DMR, or any other damage due to the deterioration of these trees and the lack of ability to determine with confidence causes of mortality.

Data analyses

All statistical analyses were performed using the SAS (version 9.1, SAS Institute Inc., Cary, N.C.) statistical program. Analysis of variance (ANOVA) using the GLM (general linear model) procedure and Tukey's honest significant difference (HSD) was used for multiple comparisons of means. The relationships between diameter and crown classes with probability of infection and number of cankers were analyzed as a randomized complete block design where study area was the block effect using the Mixed procedure. Disease incidence was calculated as the number of infected trees per number of evaluated trees per plot (excluding trees in the old dead status). Mean severity was calculated as the mean number of cankers per infected pine per plot. An infected tree had one or more branch and (or) stem cankers. Limber pine stem density was calculated on the basis of the area of the first two transects established, because only some plots had more than two transects.

Results

Limber pines were found from the lower to upper treeline, and surveyed plots ranged in elevation from 1950 m to 3155 m. Limber pine densities ranged from 54 trees/ha to 1991 trees/ha and averaged 546 trees/ha. Limber pines were found as components of many different savanna and forest communities: as the sole tree species present on 43 plots and in association with ponderosa pine on 123 plots, with lodgepole pine on 261 plots, with subalpine fir on 73 plots plots, with Douglas-fir on 111 plots, with aspen on 198 plots, with Rocky Mountain juniper on 35 plots, and with Engelmann spruce on 21 plots.

Over the course of this study, 18 719 limber pines >1.37 m in height were examined. Of the surveyed trees, very few (7.6%) were larger than 30.5 cm DBH, 23.6% were 15.3–30.5 cm DBH, most (40.9%) fell in the 5.1–15.2 cm diameter class, and the remaining 27.9% were 5.0 cm and less in diameter. The majority (81.1%) of surveyed limber pines were classified as healthy (less than 5% of crown or stem damaged or dead), 13.5% were declining or dying from various causes, and 5.4% were recently or old dead from various causes. There were no significant differences in the distribution of health status by diameter class.

White pine blister rust

Of the 17 987 limber pines evaluated for the presence of WPBR (all limber pines not classified as old dead), 2564 were infected. Of these infected trees, 25.6% had stem cankers. WPBR was present on 278 (55%) of the 504 surveyed plots. Incidence of the disease ranged from 0% to 100% of evaluated trees and averaged 15.5% over all the plots and 28.0% on the infested plots. At only one of the 504 plots, which was located on the Wind River Indian Reservation, was every evaluated tree infected with WPBR (incidence = 100%). There was variation among areas in mean incidence and severity of WPBR. Plots surveyed on the Wind River Indian Reservation had the highest mean incidence (55.9%), whereas the Sierra Madre study area had no infected limber pines (Table 1). Severity, or the mean number of total (branch and stem) cankers per infected pine, ranged from 10.4 on the Southern Medicine Bow Mountains to 1.6 on the Northern Medicine Bow Mountains (Table 2). The mean number of stem cankers per infected limber pine ranged from 0.53 at the Ferris Mountain and Laramie Peak East study areas to 0.08 at the Canyon Lakes study area.

Mean mortality, the number of dead trees per number of surveyed trees per plot, was 5.0% ± 0.3% (mean ± SE) for the 504 plots and ranged from 0% to 75.6%. Mean mortality was 4.5% on plots with WPBR, which was not significantly different than the 5.8% mean mortality found on plots without WPBR. The combined numbers of dead and declining trees did not differ significantly between plots with WPBR (7.0 ± 0.5), and plots without WPBR (7.0 ± 0.6). Of the 2520 surveyed limber pine described as declining and dying, 29.3% were infected with WPBR. Within study areas, the percentage of WPBR-infected declining and dying trees ranged from 65.8% in the Wind River study area, toward the northern extent of the survey, to ≤2.1% in the study areas at the southern extent of the study (Table 3). Of the 279 limber pines described as recently dead, 25.8% were infected with WPBR. Within individual study areas, as many as 80% of the recently killed limber pine had evidence of WPBR infection. However, in the more southerly study areas none of the recently killed limber pines had any evidence of WPBR.

Other diseases and damage

Dwarf mistletoe, primarily limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* A. Nelson ex Rydb.) and occasionally lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.), was the most commonly observed damage other than WPBR. Of the 17 987 evaluated limber pines, 9.0% were infected with dwarf mistletoe. Of the dwarf mistletoe infected trees, 7.8% were also infected by WPBR. Bark beetles (*Dendroctonus ponderosae* Hopkins and *Ips* spp.) were noted on 1.0% of evaluated limber pines. Where bark beetles were present on WPBR-infected trees, dwarf mistletoe was absent, and where bark beetles were present on dwarf mistletoe infected trees, WPBR was absent. Bark beetles were present on 1.1% of trees infected by WPBR and 2.7% of dwarf mistletoe infected trees. Other damage affecting 5% or more of the tree included abiotic damage on 1.2%, twig beetles on 1.0%, animal damage (e.g., porcupine chewing and elk or deer rubbing) on 0.6%, foliage diseases on 0.3%, fire damage on 0.2%, and root and butt decays on 0.2% of evaluated limber pines.

Ribes occurrence

Ribes were present on 239 (47.4%) of the 504 plots surveyed. Species of *Ribes* found within the 504 survey plots included *Ribes cereum* Dougl., *Ribes inerme* Rydb., *Ribes lacustre* (Pers.) Poir., and *Ribes montigenum* McClat. *Ribes cereum* was the most commonly recorded species in the plots and was established on 222 plots with densities in linear metres of live stem per hectare ranging from 2 $m \cdot ha^{-1}$ to 11 972 $m \cdot ha^{-1}$. *Ribes inerme* was the second most commonly occurring *Ribes* in plots and was recorded on 36 plots with densities ranging from 7 $m \cdot ha^{-1}$to 25 736 $m \cdot ha^{-1}$. *Ribes lacustre* and *R. montigenum* were found only rarely (four and five plots, respectively) and had lower densities relative to the other species (maximum densities were 397 $m \cdot ha^{-1}$and 4347 $m \cdot ha^{-1}$, respectively). *Cronartium ribicola* was observed on *R. inerme* but occurred rarely, likely because of

Table 1. Mean incidence of white pine blister rust at 13 study areas in Wyoming and northern Colorado, 2002–2004.

Study area[a]	n[b]	Incidence[c]	SD[d]	Range
Wind River	15	55.9	23.2	19.5–100
Muddy Mountain	20	37.1	20.5	0–72.7
Green Mountain	22	35.7	24.4	2.8–75.8
Pole Mountain, MBNF	93	30.4	22.3	0–76.5
Laramie Peak East, MBNF	29	27.2	20.4	0–91.7
Ferris Mountain	7	21.6	29.8	0–76.9
Shirley Mountains	33	19.7	19.0	0–72.4
Horse Creek, SNF	20	18.6	12.8	0–52.9
Laramie Peak West, MBNF	30	6.6	9.0	0–28.6
Canyon Lakes, RNF	75	4.1	9.6	0–47.1
Northern Medicine Bow Mountains, MBNF	60	1.2	2.9	0–12.8
Southern Medicine Bow Mountains, MBNF	69	0.9	3.9	0–25.0
Sierra Madre, MBNF	31	0.0	0	0
Total	504	15.5	21.4	0–100

[a]MBNF, Medicine Bow National Forest; SNF, Shoshone National Forest; RNF, Roosevelt National Forest.

[b]The number of plots established within each study area.

[c]Incidence is the number of infected trees/number of evaluated trees per plot averaged over all plots established in the study area.

[d]Standard deviation.

regional drought conditions, such that these data were not analyzed further.

Relationships between WPBR and tree and site variables

Diameter class was related ($p < 0.0001$) to the likelihood of a tree being infected by WPBR (Table 4). Among infected limber pines, trees >30.5 cm DBH had the greatest average number of total cankers (7.7) and a significantly lower mean number of stem cankers (0.08) than all other diameter classes. Trees in the smallest diameter class (<5 cm) had greater mean number of stem cankers (Table 4) than the other diameter classes. For infected limber pines in the smallest diameter class, the mean number of stem cankers represents 24% of mean total cankers, compared with 1% of total cankers in infected trees in the largest diameter class.

Crown class, a description of an individual tree's position in the canopy relative to adjacent trees, was also related ($p = 0.0004$) to probability of infection by WPBR (Table 5). Trees in open and dominant or codominant crown classes had a significantly greater likelihood of being infected by WPBR than trees that were in the understory or overtopped crown class. There were also differences in the mean number of cankers per infected limber pine in the various crown classes (Table 5). Trees in intermediate and overtopped or understory crown classes had fewer branch and stem cankers combined than did trees in open and dominant or codominant crown classes. The mean number of stem cankers was greater for infected limber pine in the overtopped or understory crown class than for infected trees in the dominant or codominant and intermediate crown classes. Among infected limber pines, there was a negative correlation between percent live crown and the number of stem cankers (Pearson's $r = -0.369$, $p < 0.0001$). Crown class and diameter class were moderately correlated ($r = 0.43$, $p < 0.0063$), indicating a trend for larger diameter trees to be in the open and dominant or codominant crown classes and small-diameter limber pines to be located in the understory or overtopped crown class. The lack of a strong correlation between diameter and crown class reflects the complexity of habitats and environmental conditions this species occupies.

Incidence of WPBR varied significantly by some plot variables. Incidence was negatively correlated with elevation (Table 6). Plots at elevations of less than 2590 m, of which 82% were found to be infested, had a mean incidence of 23.5% ($n = 247$) compared with the 257 plots located above 2590 m, of which 30% were infested and mean incidence was 7.7%; the difference was statistically significant at $p < 0.0001$. Incidence of WPBR was also positively correlated with geographic position, recorded in UTM coordinates, with more northerly and easterly plots having higher incidences of WPBR (Table 6). Incidence varied by slope position (Table 7) with those plots located at the bottom of slopes (valley bottom, toe slope, and foot slope positions) having greater incidences of WPBR than plots located at midslope or slope shoulder and summit positions. There were no differences among plots with different classes of slope configuration. Plots on areas described as concave had a mean incidence of 23%, but that was not significantly different from the 16.7% mean incidence found on convex plots or 13.1% incidence on plots with linear or even topography. Neither limber pine density nor slope percent were correlated with WPBR incidence. Incidence did not vary by aspect, whether defined by eight 45° or four 90° classes, although incidence was slightly higher on eastern and northern aspects than on southern and western aspects.

Incidence did not vary by canopy closure; plots described as having an open canopy had a mean incidence of 17.2% compared with 12.8% in plots described as having a closed canopy, but that difference was not statistically significant at $p = 0.05$. There were differences in incidence related to dominant trees species presence. When ponderosa pine was

Table 2. Mean white pine blister rust severity in Wyoming and northern Colorado, 2002–2004.

		Total cankers[b]		Stem cankers[c]	
Study area[a]	n^d	Mean	SD[e]	Mean	SD[e]
Southern Medicine Bow Mountains, MBNF	20	10.4	23.0	0.10	0.31
Green Mountain	295	7.6	15.1	0.20	0.57
Pole Mountain, MBNF	801	6.8	10.8	0.32	0.60
Wind River	290	6.1	9.2	0.22	0.48
Ferris Mountain	90	4.3	4.9	0.53	0.74
Shirley Mountains	274	3.2	4.4	0.44	0.58
Muddy Mountain	223	3.1	3.8	0.17	0.40
Canyon Lakes, RNF	83	2.7	2.9	0.08	0.28
Laramie Peak East, MBNF	258	2.7	3.7	0.53	0.63
Laramie Peak West, MBNF	65	2.2	2.4	0.34	0.54
Horse Creek, SNF	133	2.0	1.4	0.09	0.31
Northern Medicine Bow Mountains, MBNF	32	1.6	1.3	0.16	0.37
Sierra Madre	0	0.0	0.0	0.00	0.00

[a]MBNF, Medicine Bow National Forest; SNF, Shoshone National Forest; RNF, Roosevelt National Forest.
[b]Branch and stem cankers per infected limber pine.
[c]Stem cankers per infected limber pine.
[d]Number of WPBR-infected trees evaluated within each study area.
[e]Standard deviation.

one of the three dominant tree species on the plot, mean incidence was greater at 19.0%, whereas plots without ponderosa pine had a mean incidence of 12.6%. Incidence of WPBR was lower when lodgepole pine and subalpine fir were present (11.6% and 12.5%, respectively) as dominant species compared with plots where the lodgepole pine and subalpine fir were not dominant (20.0% and 19.1%, respectively). Density of on-plot *R. cereum* was weakly positively correlated with incidence of WPBR (Table 5), but there was no significant relationship between incidence of WPBR and density of the other species of *Ribes*. When big sagebrush (*Artemisia tridentata* Nutt.) was present as one of the three dominant understory species, mean incidence was higher (12.6%) compared with plots where big sagebrush was not a dominant understory cover (5.1%). Mean incidence was also higher (15.0%) on plots with snowberry (*Symphoricarpos albus* (L.) Blake) present as a dominant understory component.

Discussion

This survey encompassed limber pine populations throughout central and southeastern Wyoming and northern Colorado that range from heavily impacted by *C. ribicola* for over three decades to those in which the fungus has not yet become established. Because of the spatial and temporal scale of the rust distribution, these data provide insight into the potential impacts of WPBR as it continues to intensify in infested areas and spread to uninfested populations. In this relatively recently infested region of the Rocky Mountains the majority of limber pines were healthy; although 14.3% of evaluated limber pines were infected with WPBR, 9.0% were infected with dwarf mistletoe, and 1.0% had been attacked by bark beetles. In our study areas, 55% of plots contained infected limber pine, and mean incidence within infected plots was 28%. In an earlier survey of both limber and whitebark pine stands in the Intermountain West (Idaho, western Wyoming, Utah, and the Sierra Nevada Range of Nevada and California), Smith and Hoffman (2000) found that WPBR was present on 59% of established plots, and mean incidence within infected stands was 36%. In these areas closer to the point of introduction to western North America, they found a much higher rate of potentially lethal infections at 61% (Smith and Hoffman 2000) than our 26% with stem cankers among the infected white pines.

Differences among our 13 study areas in terms of both disease incidence and severity are likely related to the amount of time the pathogen has been present, differences in site suitability, and potential genetic differences in the pine and *Ribes* hosts. The role of genetic variability within populations of limber pine in susceptibility to *C. ribicola* is currently unknown but could be examined through the establishment of common garden studies that would evaluate the relative roles of site, host genetics, and pathogen genetics. WPBR incidence was generally greater in plots in northern locations where, presumably, the limber pine have been exposed to the pathogen for longer periods of time as it continues to spread south and east from its introduction in British Columbia. Several authors have reported the intensification of WPBR over time (Lachmund 1934, Fracker 1936; Van Arsdel et al. 1998; Conklin 2004). To our knowledge this was the first report of WPBR in the Northern and Southern Medicine Bow Mountains study areas, and the disease has only been detected in northern Colorado since 1998. Although the disease did not appear to be having a significant ecological effect in the Northern and Southern Medicine Bow Mountains and Canyon Lakes study areas (with 1.5%, 0.9%, and 2.1%, respectively, of declining and dying limber pines infected with WPBR at the time of this study), it is most likely that the impact of WPBR on limber pines will increase over time in these areas. WPBR is already altering forest composition through the selective removal of limber pines in more northern study areas. For example, 62.5% of the declining and dying limber pines at the Green Mountain, 54.7% in the Laramie Peak East, and 65.8% in

Table 3. Limber pine condition and percent infected by white pine blister rust in Wyoming and northern Colorado, 2002–2004.

		Declining or dying		Recent dead	
Stydy area[a]	n[b]	Count[c]	WPBR[d]	Count[e]	WPBR[f]
Horse Creek, SNF	704	31	6.5	3	0.0
Wind River	575	193	65.8	8	75.0
Muddy Mountain	637	93	46.2	5	40.0
Green Mountain	908	112	62.5	5	40.0
Laramie Peak West, MBNF	1 065	78	15.4	8	37.5
Laramie Peak East, MBNF	1 140	172	54.7	29	72.4
Ferris Mountain	391	116	47.4	19	10.5
Shirley Mountains	1 358	194	46.4	25	80.0
Pole Mountain, MBNF	3 079	447	51.7	45	35.6
Northern Medicine Bow Mountains, MBNF	2 496	271	1.5	28	0.0
Sierra Madre, MBNF	1 178	79	0.0	11	0.0
Southern Medicine Bow Mountains, MBNF	2 785	452	0.9	69	0.0
Canyon Lakes, RNF	2 403	282	2.1	24	0.0
Total	18 719	2520	29.3	279	25.8

[a]MBNF, Medicine Bow National Forest; SNF, Shoshone National Forest; RNF, Roosevelt National Forest.
[b]Number of limber pine recorded within each study area.
[c]Number of limber pine recorded as declining or dying by study area.
[d]Percentage of limber pine recorded as declining or dying infected with white pine blister rust.
[e]Number of limber pine recorded as recent dead by study area.
[f]Percentage of limber pine recorded as recent dead infected with white pine blister rust.

the Wind River study areas were infected by *C. ribicola*. Scouting reports produced by USDA Forest Service from 1951 through 1969 never reported the disease in the Green Mountain area on either *Ribes* or pine (USDA Forest Service 1950, 1951, 1959) but did report it as locally well established in areas adjacent to the Laramie Peak East area as early as 1969 (Brown 1978).

The level of mortality in limber pine detected in this study averaged 5.0% and did not differ significantly across the 504 plots in this survey between those plots with WPBR-infected trees and those plots without WPBR. However, recent mortality associated with WPBR infection was as high as 80% in the Wind River, 75% in the Shirley Mountains, and 72% in the Laramie Peak East study areas, all of which are located in the northern half of this study's extent. Overall, approximately 26% the recently killed limber pine in this study were infected by WPBR. Other studies in more northern and western North American areas have found higher total levels of mortality, including approximately 20% of whitebark pine in British Columbia with from 50% to less than 5% associated with WPBR (Campbell and Antos 2000; Zeglen 2002), 10% of whitebark pine in Oregon (Goheen et al. 2002), and 8.7% of limber and whitebark pines in the Intermountain West (Smith and Hoffman 2000). Our lower level of mortality (5%) is most likely a reflection of the shorter time of exposure to rust in our study areas. For example, none of the recent mortality in the Canyon Lakes study area, where WPBR was first reported in 1998, was associated with WPBR infection.

Relationships between WPBR and tree and site variables

Previous researchers have reported relationships similar to those we found between tree diameter and infection by WPBR (Hunt 1983; Campbell and Antos 2000; Conklin 2004). In the limber pine evaluated in this study, trees with diameters greater than 30.5 cm were more than twice as likely to be cankered than trees with diameters of less than 5 cm. The number of branch and stem cankers increased significantly with increasing diameter class. Larger diameter trees theoretically possess proportionally larger crowns and, thus, represent a larger target for intercepting windborne spores. On the other hand, the larger crowns of large-diameter trees typically consist of longer branches, increasing the distance the fungus must travel from the needle, down the branch, into the main stem and decreasing the likelihood of stem canker development. Thus, stem cankers represent a much higher proportion of the mean number of cankers for small-diameter limber pines than for larger diameter trees. Larger diameter trees are also typically older and, thus, may have been exposed to the pathogen for longer periods of time, thereby increasing the probability that they would become infected. This is probably not the case in the study areas examined here, because the majority of the trees predate the presumed arrival of the pathogen.

Significant differences in the probability of infection by WPBR and number of cankers by crown class were found in this study. Because tree diameter classes were related to crown class, it is not surprising that limber pine in the open and dominant or codominant crown classes had a significantly greater number of total cankers than did trees in the intermediate and understory crown classes. Open-grown limber pines and those in the dominant and codominant crown classes typically possess greater crown areas and experience greater crown exposure and, thus, offer a larger target for spores. On the other hand, trees in the intermediate and understory classes typically have smaller crowns that are in contact with or overtopped by the crowns of adjacent trees and so have less exposure to spores traveling on wind cur-

Table 4. Probability of white pine blister rust canker presence and mean number of white pine blister rust cankers and stem cankers by diameter class.

	All limber pine		Infected limber pine		
Diameter class (cm)	*n*	Probability of cankers	*n*	Total cankers	Stem cankers
>30.5	1371	0.30a	258	7.7a	0.08a
15.3–30.5	4290	0.25ab	782	5.3ab	0.22b
5.1–15.2	7331	0.20bc	1000	3.2bc	0.26b
≤5	4995	0.13c	524	1.7c	0.40c

Note: Values with different letters are significantly different (Tukey's HSD test, $p \leq 0.05$).

Table 5. Probability of white pine blister rust canker presence and mean number of white pine blister rust cankers and stem cankers by crown class.

	All limber pine		Infected limber pine		
Crown class	*n*	Probability of cankers	*n*	Total cankers	Stem cankers
Open	2851	0.21a	466	5.2a	0.29ab
Dominant or codominant	6153	0.23a	983	5.2a	0.20a
Intermediate	5433	0.19ab	719	2.6b	0.27a
Understory or overtopped	3434	0.14b	373	1.7b	0.40b

Note: Values with different letters are significantly different (Tukey's HSD test, $p \leq 0.05$).

rents (i.e., spores may be captured by the crowns overtopping and surrounding understory and intermediate trees). The greater number of stem cankers on infected, understory trees likely represents the smaller crowns typical of these trees and the corresponding shorter distance from needles to stem.

The relationship between elevation and incidence of WPBR found in this survey reinforces the theory that temperature and moisture regimes play a large role in the infection of both the pine or *Ribes* hosts. *Cronartium ribicola* is a macrocyclic rust, and each of its five spore stages has specific environmental conditions necessary for production and germination with some of the spore stages more sensitive to temperature and moisture requirements than others. In general, *C. ribicola* is a fungus that prefers cool, moist conditions; temperatures ranging from 1 to 24 °C and either the presence of free water or relative humidity in excess of 97% are required for spore production and germination (Hirt 1942 Van Arsdel et al. 1956; Krebill 1971; McDonald et al. 1981). Although there was a statistically significant relationship between occurrence and incidence of WPBR and elevation with higher levels of rust found at lower elevations, this relationship is unlikely to hold up in different latitudinal ranges. For example, Smith and Hoffman (2001) working in essentially the same latitudes in southern Idaho and western Wyoming found a similar relationship of higher occurrence of WPBR on plots less than 2590 m in elevation (97%) compared with plots located above 2590 m (53%). In contrast, Conklin (2004) and Geils (2000) reported a strong positive correlation between elevation and incidence of WPBR in the Sacramento Mountains of New Mexico. This relationship was attributed to the presence of *Ribes pinetorum* Greene, a highly susceptible alternate host for the pathogen, and cool, moist microclimates suitable for the pathogen found at the higher elevation sites (Geils 2000; Conklin 2004). As the above studies illustrate, the relationship between incidence of WPBR and elevation is defined by the presence of susceptible hosts and microclimatic conditions that prevent or stimulate the production and germination of rust spores rather than by elevation alone.

The significant differences in incidence related to the presence of overstory and understory species is a further reflection of the general elevation relationship found in this study. Incidence was higher when ponderosa pine was present, which occurs at lower elevations, and lower when lodgepole pine and subalpine fir were present, which occurs at higher elevations (Peet 1981). The presence of big sagebrush, a common component of lower elevation ponderosa pine forests, in the understory was also associated with significantly higher incidence of WPBR. The positive correlation between incidence of WPBR and density of *R. cereum* is of interest. Generally, *R. cereum* is not considered an important host of *C. ribicola* because it has low susceptibility to the pathogen and, when infected, supports low populations resulting in few inocula (Van Arsdel and Geils 2004). However, in reporting WPBR on limber pine in South Dakota, Lundquist et al. (1992) also report that the disease was found in *R. cereum*. Several leaves collected from a heavily infected *R. cereum* shrub at the Vedauwoo Campground in the Pole Mountain Study area were confirmed via DNA sequencing to be infected with *C. ribicola* (Detlev Vogler, USDA Forest Service, Placerville, California, personal communication). It is possible that, in the arid environs of southeastern Wyoming where *R. cereum* is the only *Ribes* species found growing among the limber pines, it plays a more significant role in the pathosystem compared with more mesic environments that support more susceptible species of *Ribes*. The role of the newly discovered alternate hosts (McDonald et al. 2006) is unclear in this pathosystem, although the presence of more susceptible species of *Ribes* within 1 km of the limber pine plots established in this study (Kearns 2005) show that *Ribes* are present throughout the range of limber pine in the study areas.

The higher incidence of rust in plots near the bottom of slopes may be related to diurnal wind patterns, in which cooler air flows into valleys and slope bases at night (Van Arsdel 1965; Whiteman 2000). This cool air accumulates at the bases of slopes and can supercool leaves, allowing dew to form and providing the conditions necessary for basidiospore production and germination (Van Arsdel 1965). Similar relationships between WPBR incidence and slope position have been reported in southern California (Kliejunas 1985) and the warmer regions of Wisconsin (Van Arsdel 1965). The lack of a relationship between slope percent, aspect, slope configuration, tree density, or crown closure and disease incidence was somewhat disappointing. We had thought that these site and stand conditions might influence rust movement and microclimate and allow for more or less infection of pines. Crown closure as a rating of stand density was apparently too coarse and variable because individual tree crown classes were related to rust incidence, but open or closed canopy structure was

Table 6. Pearson's correlation coefficients for incidence of white pine blister rust in southeastern Wyoming and northern Colorado.

		Incidence	
	n	*r*	*p* > |*r*|
Elevation (m)	504	–0.412	<0.0001
North UTM coordinates (m)	504	0.339	<0.0001
East UTM coordinates (m)	504	0.262	<0.0001
Limber pine density (trees/ha)	504	–0.092	0.0398
Percent slope	504	–0.045	0.3176
Ribes cereum density ($m \cdot ha^{-1}$)	504	0.157	0.0004
Ribes inerme density ($m \cdot ha^{-1}$)	504	0.080	0.0716

Table 7. Mean incidence of white pine blister rust by slope position.

Slope position	*n*	Incidence
Bottom slope	83	24.8a
Midslope	195	16.2b
Ridge or summit	100	12.7b
Shoulder	126	10.2b

Note: Values with different letters are significantly different (Tukey's HSD test, $p \leq 0.05$). *n*, number of plots established in each slope position category.

not. Slope percent, aspect, and slope configuration might affect relative humidity and soil moisture and, thus, spore germination. The data indicate a trend of higher incidence on plots located on concave slopes and northern and eastern slope aspects; both qualities are related to cooler, moister site conditions, which are more favorable for infection of the hosts. That these site factors were not significantly related to rust occurrence reinforces our recognition of the complexity of WPBR epidemiology and that incidence is regulated by both large and small scale factors.

Conclusions

In harsh, xeric, high-elevation ecosystems, limber pines act as pioneers ameliorating site conditions to allow the establishment of other species, or they create unique ecosystems in which they provide the only tree component (Steele 1990; Peet 1981). These white pine ecosystems are often located on steep slopes and shallow soils that are at high risk of erosion. The removal of white pines may result in the ecosystems' decreased capacity to hold snow pack, delay snowmelt, and protect watersheds (Kendall 1994; Keane et al. 1994). In addition to directly killing mature trees, WPBR can reduce regeneration of white pines by girdling cone-bearing branches or through direct mortality of seedlings. As such, WPBR can affect species diversity and alter successional pathways and spatial distributions of hosts (Castello et al. 1995; Lundquist 2005).

Krebill (1964) reported that spread of WPBR through high-elevation white pine stands in the central Rocky Mountains appeared to be slow but cautioned that the potential for impairment of the resource should not be underrated. Incidence of WPBR is currently low along the southern boundary of its distribution in southeastern Wyoming and northern Colorado. However, this information provides only a baseline of current conditions. Our surveys have shown that some areas, such as the Esterbrook Valley in the Laramie Peak East study area and the Vedauwoo area in the Pole Mountain study area, are heavily impacted by the rust, and mortality of mature trees is occurring after only two to three decades. Other areas, such as the Northern Medicine Bow Mountains, appear to be less impacted with very few trees infected by the pathogen. Although the majority of limber pines surveyed for this study were healthy, WPBR was infecting an average of 15.5% of evaluated trees. This level of infestation has been attained within the past two to four decades, and with time, the pathogen will likely spread to currently uninfested white pine populations and intensify throughout its current distribution.

Establishment of permanent monitoring plots and large-scale resurveys will be necessary to evaluate spread of the pathogen to currently uninfested areas and to determine the impacts of the disease over time. Although limber pine regeneration was not quantified in this study, it was noted on 94% of a subsample of 159 plots located in 8 of the 13 study areas. Long-term monitoring plots are currently being established throughout the range of limber pine in Colorado and Wyoming, and these will evaluate the impacts of WPBR on both regeneration and mature trees. There is a clear need to evaluate the roles and interactions of the pine and alternate hosts, microclimatic conditions, and time to aid the monitoring of this invasive, non-native pathogen and its effects on these important ecosystems.

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