NOTE TO USERS

DISSERTATION

WHITE PINE BLISTER RUST IN THE CENTRAL ROCKY MOUNTAINS: MODELING CURRENT STATUS AND POTENTIAL IMPACTS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY HOLLY S. J. KEARNS ENTITLED WHITE PINE BLISTER RUST IN THE CENTRAL ROCKY MOUNTAINS: MODELING CURRENT STATUS AND POTENTIAL IMPACTS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSPOPHY

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ABSTRACT OF DISSERTATION

WHITE PINE BLISTER RUST IN THE CENTRAL ROCKY MOUNTAINS: MODELING CURRENT STATUS AND POTENTIAL IMPACTS

The purpose of this project was to examine the current status of white pine blister rust and to develop models that predict the likelihood of disease occurrence in and damage to native white pine populations in the central Rocky Mountains. A survey of limber pine to determine the geographical distribution, incidence, and severity of white pine blister rust (WPBR), caused by the introduced forest pathogen *Cronartium ribicola*, was performed in central and southeastern Wyoming and northern Colorado in 2002-2004. WPBR was present on 55% of the 504 survey plots. Incidence, the proportion of infected trees, ranged from 0 to 100% and averaged 15.5% over all plots and 28.0% on infested plots. Diameter class and crown class were significantly related to likelihood of infection by WPBR. Incidence varied significantly by elevation and slope position and did not vary by aspect, limber pine density, slope configuration, or degree of canopy closure.

In the summers of 2002-2004, 1258 survey plots were established to determine the distribution of *Ribes* species, the alternate host for the pathogen, growing within and in the vicinity of native white pine stands in Colorado and Wyoming. Species of *Ribes* were present in all study areas. The most commonly encountered species were *R. cereum*, *R. inerme*, *R. lacustre*, and *R. montigenum.* Densities and probabilities of occurrence were related to site variables and varied by *Ribes* species. *Ribes cereum* had

higher densities in dry, open areas than in moist, densely forested areas. *Ribes inerme* had highest densities on lower elevation, riparian and wetlands areas with components of aspen and willow. *Ribes lacustre* was associated with riparian areas and closed canopy forests with components of Engelmann spruce, subalpine fir, and alder. *Ribes montigenum* had highest densities in high elevation, open stands of Engelmann spruce.

An analysis of canker growth rates was performed on 134 WPBR cankers harvested from limber pine. Mean annual total longitudinal (both up and down the branch or stem) growth rate was 8.4cm/yr. Annual proximal (toward the stem) canker growth rate averaged 4.9cm/yr, and circumferential (around the branch or stem) growth rate averaged 6.5cm/yr. Longitudinal canker growth rate varied by branch diameter, branch height, and condition of the branch distal to the canker, but did not vary by study area.

The data collected in the field surveys was used to develop a series of regression and categorical and regression tree analysis models to predict risk and hazard of WPBR in Colorado. Risk models predicting the presence of WPBR employed meteorological, *Ribes*, and tree size data and resulted in good agreement between predicted and actual presence. Models developed to predict disease pressure and hazard also employed meteorological, *Ribes*, and plot-level data. The complexity of modeling disease epidemics across vast landscapes will likely require calibration of models to specific conditions found in Colorado.

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

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). 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)). The pathogen also requires and utilizes *Ribes* species, currants and gooseberries, to complete its life cycle. In the *Ribes* host, infection is seasonal; it occurs mainly on the leaves and petioles, and thus, is shed with the leaves in autumn (Spaulding 1922). Primary infection of the pine host occurs on the needles where fungal spores land, germinate, and enter the host through the stomata. The fungus then grows within the vascular tissues into the bark, entering branches and stems (Lachmund 1933). The mycelium of the fungus grows in the intercellular spaces within the bark of white pines where the production of spores breaks through the bark causing the girdling of branches and stems, the ultimate result of

which is top kill or tree death (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 kilometers to infect a susceptible *Ribes* host (Mielke 1943).

Forest pathogens can have major effects on tree reproduction, growth, and mortality (Castello et al. 1995). Introduced forest pathogens can be particularly damaging to forest ecosystems because native tree species may have little natural resistance. White pine blister rust through its disruption of vascular tissues and bark affects white pines by reducing their growth and reproductive potential, potentially killing the pine host. After infection, mature white pines are able to survive for several years; however, they typically experience declines in cone production due to the killing by the fungus of the upper branches on which nearly all cones are produced (McCaughey 1994). White pine blister rust also acts to prevent regeneration of white pines by readily infecting seedlings and saplings causing rapid mortality (Mielke 1943). Estimates of white pine blister rust caused mortality at levels greater than ninety percent have been reported in northern Idaho and western Montana (Kendall and Arno 1990, Hagle et al. 1989).

Forest pathogens can also have ecosystem level effects on wildlife and food webs, community structure and composition, biodiversity, and ecosystem processes (Castello et al. 1995, Lundquist 2005). These indirect effects of forest pathogens occur as a result of reduced reproduction and increased mortality of the hosts. By reducing cone crops and ultimately removing the potential for seed production, white pine blister rust indirectly

effects several types of wildlife by reducing food availability for seed eaters and, consequently, for the predators of seed eaters (Mattson et al. 1992). In harsh, xeric, high elevation ecosystems, whitebark and limber pines may act as pioneers ameliorating site conditions to allow the establishment of other species; or they may 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).

The White Pines of Colorado and Wyoming

The susceptible white pines in Colorado and Wyoming are whitebark pine (*Pinus albicaulis* Engelm.), limber pine (*P. flexilis* James), Rocky Mountain (RM) bristlecone pine (*P. aristata* Engelm.) and southwestern white pine (*P. strobiformis* Engelm.). In a study of the relative resistance to *C. ribicola*, Hoff et al. (1980) determined that whitebark, limber, and southwestern white pines were among the most susceptible of the 18 species of white pines evaluated, while RM bristlecone pine exhibited a high level of resistance. These pine species are widespread in the upper subalpine and timberline zones in the mountainous regions of western North America, often occupying xeric high elevation sites where cold temperatures, short growing seasons, and soil characteristics limit the growth of other conifer species. At lower elevations and on mesic sites with deep soils, other conifer species are more competitive, and white pines are typically

considered a seral component of these systems (Kendall and Arno 1990, Arno and Weaver 1990).

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 form both lower and upper tree line. Limber pine is considered relatively shade intolerant and thus seral to many of the species with which it co-occurs, but it will co-dominate with aspen (*Populus tremuloides* Michx.), Rocky Mountain (RM) juniper (*Juniperus scopulorum* Sarg.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), lodgepole pine (*P. 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 RM bristlecone pine (Steele 1990, Peet 1981). Along the Colorado Front Range, limber pine dominates exposed, xeric sites characterized by shallow, coarse-textured soils and exposed bedrock above 2800 m, but occurs on xeric sites from 2100 to 3500 m (Peet 1981). On more mesic sites it often shares dominance with lodgepole pine, Douglas-fir, and aspen. At higher elevations, limber pine is a component of spruce-fir forests and eventually forms the upper elevational limit for forests on the most exposed and harshest sites (Peet 1981). Along the eastern face of the Medicine Bow Range in southern Wyoming, limber pine is more commonly found co-occurring with ponderosa pine, RM juniper, and Douglas-fir occupying the transition zone between grassland and forest and is rarely dominant above the lodgepole pine zone (Peet 1981). Climate data for limber pine habitats are limited, but areas east of the Continental Divide in Colorado

and Wyoming may be generally described as having a continental climate characterized by relatively little precipitation, which falls mainly during the growing season, low humidity, and broad variations in annual and diurnal temperatures (Steele 1990).

Although they have limited value as timber species, limber pines play important roles in the ecosystems in which they occur. They provide erosion protection in watersheds, increase snowpack, provide cover and a nutritious food source for wildlife including birds, rodents, and bears (Walker 1999, Steele 1990), 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).

Previously Known WPBR Distribution

Following its introduction to western North America the pathogen has spread through native white pine populations. Periodic examinations of whitebark, limber, and RM bristlecone pines and their associated *Ribes* species devoted to the detection WPBR have been conducted in Wyoming and Colorado since 1934 (Benedict 1981, Brown 1967). The first field assessments of *Ribes* and white pines in the National Forests and National Parks of Colorado and Wyoming were implemented in 1934 by Blister Rust Control program crews (Benedict 1981). *Ribes* eradication work occurred on a small scale in selected areas in these states through the mid-1960s (Benedict 1981). From the 1950s through 1970 regular detection and scouting of white pines and *Ribes* by USDA Forest Service pathologists and crews occurred at specific sites in Wyoming and selected areas of Colorado including Rocky Mountain National Park and the Roosevelt National Forest

(N.F.). *Cronartium ribicola* infection on *Ribes* was first observed in Wyoming near Mammoth Hot Springs in Yellowstone National Park in 1944 (USDA Forest Service 1950). Rust on *Ribes petiolare* was observed west of Lander in 1949 (USDA Forest Service 1950). In 1950, blister rust was observed for the first time infecting pine in Park County, Wyoming (USDA Forest Service 1951), which is located in the northwest portion of the state and includes portions of Yellowstone National Park. In 1966, the first WPBR infection in pine was reported at the northern edge of the Shoshone N.F., with an associated approximate age of infection of 1941 (Brown 1967). WPBR infection centers located along the east side of the Bighorn Mountains were first reported in a 1959 scouting report (USDA Forest Service 1959) and were confirmed in 1966. At that time, Brown (1967) estimated that the cankers on limber pine ranged from 5 to 25 years in age. Surveys in 1969 found that the pathogen was locally well established in some limber pine populations in the Laramie Peak area of the Medicine Bow N.F., west of Wheatland, Wyoming (Brown 1978). *Cronartium ribicola* was identified from a *Ribes* sample collected near Laramie, Wyoming, in 1952 (USDA Forest Service 1952). A gap in documented surveys of Wyoming and Colorado for WPBR apparently occurred between the early 1970s and late 1990s. WPBR cankers were evident though sparse on limber pine in a 1982 examination at the Pole Mountain area of the Medicine Bow N.F., east of Laramie, Wyoming (B.W. Geils, personal communication). In 1998, plots established at the Pole Mountain area of the Medicine Bow N.F. found that 50% of 105 examined limber pines were infected with WPBR (Harris 1999).

WPBR was first reported in Colorado in 1998 on the Roosevelt N.F., and all infected limber pines were located within an area approximately 18 km south of the Wyoming border (Johnson and Jacobi 2000). The pathogen had previously been reported in limber pine along its easternmost distribution in 1992 in North Dakota (Draper and Walla 1993) and South Dakota (Lundquist et al. 1992). In 2003, isolated WPBR infestations were discovered in the Wet and Sangre de Cristo Mountains of southern Colorado, more than 450 km from other known infections. Limber pines were infected in these latter areas, and the first sightings of infected RM bristlecone pine were noted (Blodgett and Sullivan 2004), heightening concerns about this species and other high elevation white pines. WPBR has the potential to spread naturally or be introduced throughout the range of white pines in Colorado, which includes scattered populations of limber, southwestern white, and RM bristlecone pines from Wyoming to the Colorado / New Mexico state line (Johnson and Jacobi 2000).

Although limber pine is an important component of many forested ecosystems in Wyoming and Colorado very little is known about its health status. The objectives of this study were to: 1) examine the condition of limber pine throughout central and southeastern Wyoming and northern Colorado, 2) determine the geographical distribution, incidence, and severity of WPBR, 3) determine if incidence of WPBR varies in relation to site variables and tree characteristics, and 4) provide information to aid in the development of predictive models.

Methods

Study areas

Surveys occurred on 13 study sites defined by government management units and geographic locations, including (Figure 1.1): the Horse Creek area of the Shoshone National Forest (SNF), Wyoming; Wind River Indian Reservation, Wyoming lands managed by the Bureau of Indian Affairs (BIA); Green Mountain, Ferris Mountain, Shirley Mountains, and Muddy Mountain, Wyoming lands managed by the Bureau of Land Management (BLM); Laramie Peak East and West sections, Sierra Madre, North and South sections of the Snowy Range, and Pole Mountain areas of the Medicine Bow National Forest, Wyoming; and the Canyon Lakes District of the Roosevelt National Forest, Colorado. These study sites were selected to encompass areas in Wyoming where the pathogen has been known to be present for up to 40 years (USDA Forest Service 1950, Brown 1967) and also in areas in northern Colorado where the pathogen has been newly reported (Johnson and Jacobi 2000).

Stand selection

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 (RMRIS) database. Digital Ortho Quadrangles were obtained from the Roosevelt and Medicine Bow National Forests and maps created to direct the sampling effort in these areas. In the first three areas sampled (Pole Mountain, Northern Snowy Range and Southern Snowy Range - Figure 1.1) all stands with records

of limber pine were stratified by elevation and topographic relative moisture index (TRMI, Parker 1982) based on data available from RMRIS. Attempts were made to sample equally in each of four classes: low elevation - mesic; low elevation - xeric, high elevation – mesic, and high elevation – xeric. The lack of correspondence between actual site conditions and stratification classes halted the pre-stratified survey after the first three study areas. Post-stratification was then 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. Surveyed stands were within three kilometers of a road to limit travel time between stands and maximize the number of plots established. Paper maps were obtained for areas managed by Bureau of Land Management and Bureau of Indian Affairs. Surveys in non-Forest Service managed areas were directed to locations recommended by employees familiar with the areas as having significant populations of limber pine, again ignoring WPBR conditions.

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, after establishing five transects, 30 limber pine were not observed no more transects were established. Pine transects were 61 x 4.6 m and were located along random bearings through the stand. The GPS coordinates of the starting point of each transect were recorded. 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 (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, recent 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/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 damages affecting 5% or more of the tree. Trees growing in clumps were considered individual stems if they were distinct at 1.37m height and were growing at an angle greater than 45° above horizontal. Binoculars were used to examine the crowns of trees for cankers and other damages. 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. 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 damages due to the deterioration of these trees and the lack of ability to determine with confidence causes of mortality.

At the end of each pine transect, along the same bearing, a *Ribes* transect (30.5 x 4.6 m) was established in which the *Ribes* species present, total number of stems or bushes,

average number of stems per bush, average stem length, percent of stems or bushes with rust, and average percent of leaves per stem of bush with rust were recorded. From these data densities of *Ribes* by species in linear meters of live stem per hectare were calculated. Subsequent pine transects were started at the end of the *Ribes* transect along another random bearing. 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.

Data Analyses

Disease incidence was calculated as the number of infected trees/number of evaluated trees (excluding trees in the old dead status). Limber pine stem density was calculated on the basis of the area of the first two transects established, as only some plots had more than two transects. All statistical analyses were performed utilizing the SAS (version 9.1, SAS Institute Inc.) statistical program. Tukey's honest significant difference (HSD) was used for multiple comparisons of means because it is recommended for unequal sample sizes and is considered conservative in that it has a low type I error rate (falsely rejecting the null hypothesis) and shows fewer significant differences (P. Chapman, personal communication) such that variables are more likely to be useful in model building.

Results

Limber pines were found from lower to upper treeline, and surveyed plots ranged in elevation from 1,950 to 3,155 m. Limber pine densities ranged from 54 to 1,991 trees per hectare (tph) and averaged 546 tph. Limber pines were found as components of many different savanna and forest communities; as the sole tree species present on 43 (9%) plots, and in association with ponderosa pine on 123 (24%), with lodgepole pine on 261 (52%), with subalpine fir on 73 (14%) plots, with Douglas-fir on 111 (22%) plots, with aspen on 198 (39%) plots, with Rocky Mountain juniper on 35 (7%), and with Engelmann spruce on 21 (4%) plots.

Over the course of this study, 18,719 limber pine >1.37m in height were examined. Very few surveyed trees (1,420 (7.6%)) were larger than 30.5 cm DBH (Figure 1.2) and most fell in the 5.1 – 15.2 cm diameter class. The majority (81.1%, Figure 1.3) of surveyed limber pines was classified as healthy (less than 5% of crown or stem damaged or dead), 13.5% were declining or dying, and 5.4% were dead. There were no significant differences in the distribution of health status by diameter class (Figure 1.4). Mean mortality, the number of dead trees per number of surveyed trees per plot, was 5.0% (standard error (SE) 0.3) 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 average 5.8% mortality found on plots without WPBR. However, the mean number of dead trees per plot was significantly higher for plots with no evidence of WPBR at 2.4 (SE 0.2) compared to plots with WPBR at 1.7 (SE 0.2), which may be attributable to the slightly, but not significantly, higher limber pine densities found on plots without WPBR. The

numbers of dead and declining trees together did not differ significantly between plots with WPBR, mean 7.0 (SE 0.5), and plots without WPBR, mean 7.0 (SE 0.6). Of the 279 limber pines described as recent dead, 25.8% were infected with WPBR; 23.8% had stem cankers and 9.3% had branch cankers.

WPBR was found in all study areas except the Sierra Madre (Table 1.1). 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, located on the Wind River Reservation, was every evaluated tree infected with WPBR (incidence=100%). There were significant differences among sites in incidence of WPBR (Table 1.1). The plots on the southwestern Wind River Indian Reservation had significantly higher mean incidence than any other study sites. There were also significant differences in severity between sites. Mean number of total cankers per infected pine, including branch and stem cankers, ranged from 10.4 on the Southern Snowy Range to 1.6 on the Northern Snowy Range (Table 1.2). The mean number of stem cankers per infected limber pine also differed significantly among study sites (Table 1.2), ranging from 0.53 at the Ferris Mountain and Laramie Peak East study sites to 0.08 at the Roosevelt National Forest. Of the 17,987 limber pines evaluated for the presence of WPBR (all limber pines not classified as old dead), 2,564 were infected. Of these infected trees, 657 (25.6%) had stem cankers.

Dwarf mistletoe, primarily limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* A. Nelson ex Rydberg) and occasionally lodgepole pine dwarf mistletoe (*A. americanum* Nuttall ex Engelmann), was the most commonly observed damage other than WPBR. Of the surveyed limber pines, 1,610 (8.6%) had dwarf mistletoe, 732 (3.9%) were not evaluated because they were classified as old dead, and 16,377 (87.5%) had no evidence of dwarf mistletoe infection. Mild dwarf mistletoe infestations (DMR 1 and 2) were found on 3.0% (543) of evaluated limber pine, moderate infestations (DMR 3 and 4) were found on 2.8% (499) of evaluated trees, and severe infestations (DMR 5 and 6) were found on 3.2% (568) of evaluated limber pine. Bark beetles were noted on 181 (1.0%) of evaluated limber pine. Other damages affecting 5% or more of the tree were found rarely and include abiotic damages on 221 (1.2%), twig beetles on 185 (1.0%), animal damage (i.e. porcupine chewing or elk/deer rubbing) on 109 (0.6%), foliage diseases on 58 (0.3%), fire damage on 30 (0.2%), and root and butt decays on 39 (0.2%) evaluated limber pines.

Where bark beetles were present on WPBR infected trees, dwarf mistletoe was generally absent, and where bark beetles were present on dwarf mistletoe infected trees, WPBR was absent (Table 1.3). Bark beetles were present on 1.1% of trees infected by WPBR and 2.7% of dwarf mistletoe infected trees. The highest counts of bark beetle infested trees, 108 or 59.7%, were those trees that had neither WPBR nor dwarf mistletoe. Of the dwarf mistletoe infected trees, 125 (7.8%) were also infected by WPBR; while the vast majority 1485 (92.2%) had no evidence of WPBR infection. Severe infestations of dwarf mistletoe were recorded on 568 limber pines, of which 4.4% also had bark beetles and

3.9% had WPBR. For the 499 moderately dwarf mistletoe infected trees, 3.4% had evidence of bark beetles, and 6.4% had WPBR. In the 543 mildly infested dwarf mistletoe trees, 0.4% had evidence of bark beetle attack and 13.1% had WPBR cankers.

Ribes were present on 239 (47.4%) of the 504 plots surveyed. Species of *Ribes* found within the 504 survey plots included *Ribes cereum*, *R. inerme*, *R. lacustre*, and *R. montigenum*. *Ribes cereum* was the most commonly recorded species in the plots and was established on 222 (44.1%) of the plots with densities in linear meters of live stem per hectare (m/ha) ranging from 2 to 11,972. *Ribes inerme* was the second most commonly occurring *Ribes* in plots and was recorded on 36 (7.1%) of plots with densities ranging from 7 to 25,736 m/ha. *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 and 4,347 m/ha, respectively).

Due to the significant differences among the study sites in terms of WPBR incidence and severity, we now provide a detailed summary of conditions at each of the study sites that may be useful for future monitoring efforts and studies of disease dynamics.

Ferris Mountain

During the summer of 2003, seven white pine plots were established in the Ferris Mountain study area. A total of 391 limber pines were examined with 62.9% (246) classified as healthy, 29.7% (116) as declining or dying, and 7.4% (29) as dead. Limber pines were located in a variety of forest types that ranged in elevation from 2,182 to

2,395 m. Limber pine density ranged from 416 to 1,060 tph and averaged 663 tph. On two plots (29%) limber pine was the only tree species present, and it co-occurred with Douglas-fir on 57%, with RM juniper on 57%, and with aspen on 14% of established plots. All seven plots had *Ribes* present; *R. cereum* and *R. inerme* were the only species of *Ribes* recorded throughout the study area. *Ribes cereum* was present on 4 (57%) of plots, and *R. inerme* was present on 4 (57%) of established plots.

There was a moderate occurrence of WPBR throughout this study area with 57% (4 of 7) of pine plots sampled containing limber pine infected with the pathogen. Plots with WPBR were located in the northern portion of the study area (Figure 1.5). Incidence of WPBR averaged 21.6% (Table 1.1) of the limber pines in the seven sampled plots; the maximum percent of trees infected in any one plot was 76.9. Of the 90 limber pine with WPBR, 35 (38.9%) had stem cankers; the mean number of stem cankers per infected limber pine was 0.53, one of the highest average severities recorded for all study areas (Table 1.2). The mean number of total cankers, includes both stem and branch cankers, per infected limber pine was 4.3 (Table 1.2). Dwarf mistletoe was present on 23% of evaluated limber pine, making it the most commonly recorded damage after WPBR. Bark beetles were recorded on 5 (1%) of evaluated limber pines. Of the 90 trees with WPBR cankers, 20 (22%) also had dwarf mistletoe infections and 3 (3%) had evidence of bark beetles. Of the declining and dying limber pine, 29% (34) were infected with WPBR. Of the 19 recently killed limber pine evaluated, 84% were attributed to dwarf mistletoe and 16% to bark beetles. No evidence of WPBR was observed on recently killed trees.

Green Mountain

We established 22 white pine plots in the Green Mountain study area during the summer of 2002. Nine hundred and eight limber pines were recorded with 84.1% (764) described as healthy, 12.3% (112) as declining or dying, and 3.5% (32) as dead. Limber pine plots ranged in elevation from 2,185 to 2,774 m. Limber pine was the sole tree component in 41% (9) of the established plots and co-occurred with lodgepole pine on 41%, with aspen on 23%, with RM juniper on 18%, and with subalpine fir on 5% of surveyed plots. Only 3 (13.6%) of the 22 plots had *Ribes* species present. *Ribes cereum* was present on three plots, and *R. inerme* was present on one plot.

There was a high occurrence of WPBR throughout this study area with 100% of limber pine plots sampled infested with the disease. Plots with WPBR were located throughout the study area (Figure 1.6). WPBR was affecting an average 35.7% of the limber pines in sampled plots (Table 1.1); the maximum percent of trees infected in any one plot was 75.8. Of the 295 pines with WPBR, 15.6% (46) had stem cankers, and the mean number of stem cankers per infected limber pine was 0.20 (Table 1.2). The mean number of branch and stem cankers combined per infected white pine was 7.6. Dwarf mistletoe was affecting the health of 5% (42) of evaluated limber pines. Bark beetles were noted on only 2 of the evaluated limber pines. Of the 295 trees with WPBR cankers, 24 (8%) were also infected with dwarf mistletoe and 2 (1%) had been attacked by bark beetles. Of the declining and dying limber pines, 55% (62) were infected with WPBR and the remaining trees were experiencing damage due to dwarf mistletoe infections, competition, abiotic

agents, and twig beetles. Two of the five recent dead limber pines had been killed by WPBR and three had dwarf mistletoe infections.

Horse Creek

Our survey established 20 white pine plots in the Horse Creek area of the Shoshone National Forest during the summer of 2003. A total of 704 limber pines were examined with 93.3% (657) classified as healthy, 4.4% (31) as declining or dying, and 2.3% (16) as dead. Limber pines were located in a variety of forest types that ranged in elevation from 2,336 to 2,731 m. Limber pine density ranged from 215 to 1,256 tph and averaged 580 tph. On 15% of plots limber pine was the only tree species present, and it co-occurred with lodgepole pine on 45% of plots surveyed, with Douglas-fir on 35%, with Engelmann spruce on 30%,with aspen on 20%, with subalpine fir on 20%, and with RM juniper on 5% of established plots. *Ribes* were recorded on only 25% (5) of survey plots. *Ribes cereum* was present on 15% of plots, *R. inerme* on 5%, and *R. montigenum* on 10% of established plots.

Overall occurrence of WPBR was high; 95% (19 of 20) of pine plots sampled had limber pine infected with the disease. Plots with WPBR were located throughout the study area (Figure 1.7). On average, WPBR affected 18.6% (Table 1.1) of the limber pines in sampled plots; the maximum percent of trees infected in any one plot was 52.9. Of the 133 sampled trees that had WPBR, 11 (8.3%) had stem cankers with a mean number of stem cankers per infected pine of 0.09, while mean total cankers per infected pine was 2.0 (Table 1.2). Of the declining and dying limber pines, 2 (6%) had WPBR, while the

remainder had damages attributed to wild animals, competition, abiotic stresses, and twig beetles. Of the recently killed limber pines, none had evidence of WPBR. Neither dwarf mistletoe nor bark beetles were detected on any of the evaluated limber pines.

Laramie Peak East

During the summer of 2002, 29 white pine plots were established in the Laramie Peak East study area of the Medicine Bow National Forest. A total of 1,140 limber pines were observed within the established plots with 73.7% (840) described as healthy, 15.1% (172) as declining and dying, and 11.2% (128) as dead. Limber pines were located in a variety of forest types that ranged in elevation from 2,212 to 2,573 m. Limber pine density ranged from 144 to 1,704 tph and averaged 637 tph. Limber pine was the sole tree species present on one of the 29 plots established and co-dominated with ponderosa pine on 69%, with aspen on 52%, with lodgepole pine on 41%, with Douglas-fir on 14%, and with RM juniper on 10% of plots. *Ribes cereum* was the only *Ribes* species found growing amongst the surveyed limber pines and was present on 12 (41%) of the plots.

WPBR was present on 28 (97%) of the 29 plots established in the Laramie Peak East study area. Plots with WPBR were located throughout the study area (Figure 1.8). Average incidence of WPBR on the 29 plots was 27.2% (Table 1.1); the maximum percent of trees infected in any one plot was 91.7. Stem cankers were present on 47.7% (123) of the 258 infected limber pines. Mean number of stem cankers per infected pine was 0.53, one of the highest average severities recorded for all study areas and the mean number of total cankers per infected limber pine was 2.7 (Table 1.2). Dwarf mistletoe

infestations occurred on 8% (81) of evaluated white pines and were the second most common cause of damage. Evidence of bark beetle attacks was present on 6 (1%) of evaluated limber pines. Dwarf mistletoe infections were present on 12 (5%) of the 258 WPBR infected pines and bark beetles were evident on 5 (2%). Of the 172 limber pine described as declining or dying, 85 (49%) were infected with WPBR, 29 (17%) had dwarf mistletoe, and 5 (3%) had been attacked by bark beetles. The remaining declining and dying limber pines were experiencing damages due to wild animals, competition, abiotic stresses, and twig beetles. Of the 29 recently dead limber pines recorded, 21 (72%) had evidence of WPBR infection and none had dwarf mistletoe.

Laramie Peak West

During the summer of 2002, 30 plots were established in the Laramie Peak West study area of the Medicine Bow National Forest. A total of 1,065 limber pines were examined with 87.3% (930) classified as healthy, 7.3% (78) as declining or dying, and 5.4% (57) as dead. Limber pines were located in a variety of forest types that ranged in elevation from 2,326 to 2,758 m. Limber pine density ranged from 269 to 1,094 tph and averaged 511 tph. On only one plot was limber pine the only tree species present, otherwise it co-occurred with lodgepole pine on 80% (24) of surveyed plots, with subalpine fir on 33% (10), with aspen on 30% (9), with Douglas-fir on 27% (8), with ponderosa pine on 13% (4), with Engelmann spruce on 10% (3), and with RM juniper on 7% (2) of established plots. Only seven plots had *Ribes* present, and *R. cereum* and *R. lacustre* were the only species of *Ribes* recorded throughout the study area. *Ribes cereum* was present on 6 (20%) of plots, and *R. lacustre* was present on 1 (3%) plot.

There was a moderate occurrence of WPBR throughout this study area with 60% (18 of 30) of pine plots sampled containing limber pine infected with the pathogen. Plots with WPBR were located throughout the study area (Figure 1.9), with incidence appearing to increase to the southeast. Incidence of WPBR averaged 6.6% (Table 1.1) of the limber pines in the 30 sampled plots; the maximum percent of trees infected in any one plot was 28.6. Of the 65 limber pine with WPBR, 20 (30.1%) had stem cankers. The mean number of stem cankers per infected limber pine was 0.34, and the mean number of total cankers, including both stem and branch cankers, per infected limber pine was 2.2 (Table 1.2). Dwarf mistletoe was present on 2.1% (21) of evaluated limber pine. Evidence of bark beetles was recorded on 11 (1.1%) of limber pines. None of the limber pines infected with WPBR were also infected with dwarf mistletoe, but 6% had also been attacked by bark beetles. Of the declining and dying limber pine, 10% (8) were infected with WPBR, 10% (8) had been attacked by bark beetles, and 5% (4) had dwarf mistletoe infections. The remaining declining and dying limber pines had damages attributed to foliage diseases, fire, wild animals, abiotic stresses, competition, and twig beetles. Of the eight recently dead limber pine evaluated, 50% were attributed to WBPR and 38% to bark beetles.

Muddy Mountain

We established 20 white pine plots in the Muddy Mountain study area during the summer of 2003. Six hundred and thirty-seven limber pines were recorded with 82.1% (523) described as healthy, 14.6% (93) as declining or dying, and 3.3% (21) as dead. Limber

pine plots ranged in elevation from 1,948 to 2,516 m. Limber pine was the sole tree component in 20% (4) of the established plots and co-occurred with aspen on 45%, with lodgepole pine on 35%, with ponderosa pine on 25%, with Douglas-fir on 15%, and with RM juniper on 15% of surveyed plots. *Ribes cereum* was the only species of *Ribes* found growing amongst the limber pines, and it was recorded on only 3 (15%) of the 20 plots.

There was a high occurrence of WPBR throughout this study area with 95% (19 of 20) of limber pine plots sampled infested with the disease. Plots with WPBR were located throughout the study area (Figure 1.10). WPBR was affecting an average 37.1% of the limber pines in sampled plots (Table 1.1); the maximum percent of trees infected in any one plot was 72.7. Of the 223 pines with WPBR, 15.7% (35) had stem cankers, and the mean number of stem cankers per infected limber pine was 0.17 (Table 1.2). The mean number of total cankers per infected white pine was 3.1. Dwarf mistletoe was recorded on 3.5% (22) of evaluated limber pines and bark beetles were detected on 0.6% (4). Of the 223 limber pines with WPBR infections, 6 (3%) were also infected with dwarf mistletoe and 2 (1%) had been attacked by bark beetles. Of the declining and dying limber pines, 34% (32) were infected with WPBR, 13% (12) were infected with dwarf mistletoe, and 1% (1) has been attacked by bark beetles. Other damages recorded on declining and dying limber pines were attributed to sucking insects, wild animals, competition, abiotic stresses, and twig beetles. Two of the five recent dead limber pines had been killed by WPBR, the remaining three had evidence of bark beetle attacks.

Northern Snowy Range

Our survey established 60 white pine plots during the summers of 2002 and 2003. A total of 2,496 limber pines were examined with 83.4% (2081) classified as healthy, 10.9% (271) as declining or dying, and 5.8% (144) as dead. Limber pines were located in a variety of forest types that ranged in elevation from 2,482 to 3,155 m. Limber pine density ranged from 126 to 1,991 tph and averaged 626 tph. On 7% of plots limber pine was the only tree species present, and it co-occurred with lodgepole pine on 67% of plots surveyed, with aspen on 35%, with subalpine fir on 33%, with Engelmann spruce on 10%, with Douglas-fir on 5%, and with RM juniper on 5% of established plots. *Ribes* were recorded on 42% (25) survey plots. *Ribes cereum* was present on 37% of plots, *R. lacustre* on 2%, and *R. montigenum* on 5% of established plots.

Overall occurrence of WPBR was low, only 22% (13 of 60) of pine plots sampled had limber pine infected with the disease. All plots with WPBR were located along the northern edge of the study area (Figure 1.11). Accessibility to areas with white pines was limited in the northern portion of the study area, so the full extent of the disease is not known. On average, WPBR affected 1.2% of the limber pines in sampled plots; the maximum percent of trees infected in any one plot was 12.8. Of the 32 trees sampled that had WPBR, 5 (15.6%) had stem cankers with a mean number of stem cankers per infected pine of 0.16 (Table 1.2). The mean number of branch and stem cankers combined per infected pine was 1.6 (Table 1.2). Dwarf mistletoe was present on 12% of evaluated limber pines. Evidence of bark beetle attacks was present on 0.5% of limber pines. Of the WPBR infected limber pines, 7 (22%) were also infected with dwarf

mistletoe, and none had evidence of bark beetle attack. The association between bark beetles and dwarf mistletoe was 42% bark beetle infested trees also were infected with dwarf mistletoe, while 2% of dwarf mistletoe infected trees had evidence of bark beetles. Of the declining and dying limber pines, 62% (167) had dwarf mistletoe, 1% (4) had been attacked by bark beetles, and only 1 (0.4%) had WPBR. Other damages recorded on declining and dying limber pines included sucking insects, root diseases, foliar pathogens, fire, wild animals, abiotic stresses, competition, and twig beetles. Of the recently killed limber pines, none had evidence of WPBR, 57% had dwarf mistletoe, and 29% had evidence of bark beetle attack.

Pole Mountain

During the summer of 2002, we established 93 white pine plots in the Pole Mountain study area. A total of 3,079 limber pines were examined with 81.8% (2520) classified as healthy, 14.5% (447) as declining or dying, and 3.6% (112) as dead. Limber pines were located in a variety of forest types that ranged in elevation from 2,326 to 2,719 m. Limber pine density ranged from 54 to 1,615 tph and averaged 425 tph. On 2% of plots limber pine was the only tree species, and it co-occurred with ponderosa pine on 60% of plots surveyed, with aspen on 46%, with lodgepole pine on 35%, with Douglas-fir on 20%, and subalpine fir on 8% of established plots. All but 19 (20%) of the 93 plots had at least one species of *Ribes* present. *Ribes cereum* was present on 73 (78%) of plots and *R. inerme* was present on 14% of established plots.

There was a high occurrence of WPBR throughout this study area with 91% (85 of 93) of pine plots sampled containing limber pine infected with the pathogen. Plots with WPBR were located throughout the study area (Figure 1.12). Incidence of WPBR averaged 30.4% of the limber pines in the 93 sampled plots; the maximum percent of trees infected in any one plot was 76.5. Of the 801 limber pine positive for WPBR, 209 (26.1%) had stem cankers, and the mean number of stem cankers per infected limber pine was 0.32 (Table 1.2). The mean number of total cankers per infected limber pine was 6.8. Dwarf mistletoe was present on 2.8% (84) of evaluated limber pine. Evidence of bark beetle attack was present on three limber pines infected with WPBR and on none of the limber pine infected with dwarf mistletoe. Both dwarf mistletoe and WPBR were present on 18 trees, which accounted for 21% of the dwarf mistletoe infected trees and 2% of the WPBR infected trees. Of the declining and dying limber pine, 44% (198) were infected with WPBR. Other damages recorded on declining and dying limber pines included sucking insects, root diseases, foliar pathogens, wild animals, abiotic stresses, competition, and twig beetles. Of the limber pine described as recent dead, 31% (14 of 45) were attributed to WPBR, and none had evidence of bark beetle attack or dwarf mistletoe infection.

Roosevelt National Forest

In the summer of 2003, 75 plots were established throughout much of the limber pine habitat in the Canyon Lakes District of the Roosevelt National Forest. Through that survey the health of 2,403 limber pines greater than 1.37 m in height was evaluated. The vast majority of limber pines were described as healthy (83.3%), while 11.7% were

described as declining or dying, and 5% as dead. The plots ranged in elevation from 2,438 m 3,136 m. Limber pine was the sole tree component on 2 (2.7%) of the 75 established plots, otherwise it co-dominated with lodgepole pine on 63%, with Douglas-fir on 43%, with ponderosa pine on 39%, with aspen on 33%, with subalpine fir on 9%, and with Engelmann spruce on 1% of the surveyed plots. The species of *Ribes* recorded growing amidst the limber pine were *R. cereum*, present on 30 (40%) of plots, and *R. inerme*, present on 8 (11%) of plots.

Occurrence of WPBR was generally low, 20 of the 75 plots (27%) contained diseased limber pine. Plots with WPBR were concentrated in the northern end of the study area (Figure 1.13). Incidence of WPBR averaged 4.1% within surveyed plots (Table 1.1). The highest incidence recorded in any one plot was 47.1%. Of the 83 trees positive for WPBR, 7 (8.3%) had stem cankers; the mean number of stem cankers per infected limber pine was 0.08 (Table 1.2). The mean number of branch and stem cankers per infected limber pine was 2.7. Dwarf mistletoe was the most commonly recorded agent causing damage to trees and was affecting 8.8% (203) of evaluated limber pines. Bark beetle attacks were recorded for 21 (0.9%) of evaluated limber pines. None of the WPBR infected pines had evidence of either bark beetles or dwarf mistletoe. However, 52% of bark beetle infested trees were infected by dwarf mistletoe. In only 1% of the declining and dying limber pine was the decline attributed to WPBR; 54% were infected with dwarf mistletoe and 2% had evidence of bark beetle attacks. Other damages recorded on declining and dying limber pines included defoliating insects, foliar pathogens, stem decays, fire, wild animals, abiotic stresses, competition, and twig beetles. None of the

recent dead limber pines were infected with WPBR. Recent dead limber pines had evidence of dwarf mistletoe (67%) and secondary bark beetle attack (63%).

Shirley Mountains

We established 33 white pine plots in the Shirley Mountain study area during the summer of 2002 in which 1,358 limber pines > 1.37 m in height were evaluated. Of the evaluated limber pine, 80.6% were healthy, 14.3% was described as declining or dying, and 5.1% were dead. Surveyed limber pines ranged in elevation from 2,263 to 2,667 m. Limber pine was the only tree component on 42% of the plots and elsewhere co-dominated with RM juniper on 27%, with lodgepole pine in 21%, with aspen on 15%, with subalpine fir in 9% and with ponderosa pine in 6% of surveyed plots. *Ribes cereum* was present on 13 (39%) of the pine plots and *R. inerme* was present on 5 (15%).

Overall, there was a high occurrence of WPBR throughout this study area with 91% (30) of limber pine plots sampled infested with the disease. Plots with WPBR were located throughout the study area (Figure 1.14). On average, WPBR was affecting 19.7% of the limber pines in sampled plots (Table 1.1); the maximum percent of trees infected in any one plot was 72.4. Of the 274 limber pine diagnosed with WPBR, 108 (39.4%) had stem cankers. The mean number of stem cankers among infected limber pine was 0.44, which was among the highest levels found at any of the study sites (Table 1.2). The mean number of branch and stem cankers combined per infected limber pine in the Shirley Mountains was 3.2 (Table 1.2). The deaths of 18 of the 25 (72%) recent dead limber pine were attributable to WPBR. Among the declining and dying limber pine, 37% had

WPBR, 23% had dwarf mistletoe, 4% had been attacked by bark beetles, 7% had root disease, 8% had twig beetles, 16% had abiotic damage, and the remainder had damages attributed to foliar pathogens and competition. Dwarf mistletoe was present on 7.7% (101) of all evaluated limber pines and evidence of bark beetles was present on 1.0% (13). Of the limber pines infected with WPBR, 8 (3%) had evidence of bark beetles, 12 (4%) were also infected with dwarf mistletoe, and none had evidence of both. Bark beetles were associated with only one of the dwarf mistletoe infected limber pines.

Sierra Madre

Our survey established 31 white pine plots on the Sierra Madre area of the Medicine Bow National Forest during the summers of 2002 and 2003 and evaluated 1,178 limber pines. The majority (87.6%) of sampled trees was classified as healthy, 6.7% were declining or dying, and 5.7% were dead. Sampled limber pines ranged in elevation from 2,480 to 2,929 m. Limber pine was the only tree component on 16% of the sampled plots and it co-dominated with lodgepole pine on 65%, with aspen on 52%, and with subalpine fir on 39% of the sampled plots. 75% of stands examined were dominated by limber pine, 21% by lodgepole pine, and 4% by subalpine fir. The only species of *Ribes* found to be growing amid the limber pines was *R. cereum*, which was present on 18 (58%) of the plots.

There was no indication of the presence of WPBR in any sampled pine plots. Plots were established along the eastern portion of the Sierra Madre Range (Figure 1.15). The most commonly reported damages on the declining and dying limber pines were twig beetles

(16%), abiotic stress (15%), competitive stress (11%), and dwarf mistletoe (10%). Other damages recorded on the declining and dying limber pines included bark beetles, sucking insects, boring insects, foliar pathogens, and wild animals. Dwarf mistletoe occurred rarely in the sampled plots and was present on only 1.4% of evaluated limber pine. The presence of bark beetles was evident on 25 (2.2%) of evaluated limber pines. Of the recent dead limber pines, the majority (73%) had evidence of bark beetle attack. None of the limber pines with bark beetles were infected with dwarf mistletoe.

Southern Snowy Range

During the summers of 2002 and 2003, 69 white pine plots were established in the Southern Snowy Range study area of the Medicine Bow National Forest. The majority (77.1%) of the 2,785 limber pines evaluated was described as healthy, 16.2% were declining and dying, and 6.7% were dead. Plots were established within a variety of forest types and ranged in elevation from 2,425 to 2,941 m. Limber pines were found co-dominating with lodgepole pine in 71% of plots, with aspen in 55%, with Douglas-fir in 32%, with ponderosa pine in 12%, with subalpine fir in 10%, and with RM juniper in 4% of sampled plots. Three species of *Ribes* were recorded in the plots: *Ribes cereum* (38% of plots), *R. inerme* (3% of plots), and *R. lacustre* (1% of plots).

There was a low occurrence of WPBR throughout the southern Snowy Range study area; 7% of plots sampled had limber pine infected with the disease. All plots with WPBR were located on the eastern side of the study area (Figure 1.16). On average, WPBR was affecting 0.9% of the limber pines in sampled plots (Table 1.1); the maximum percent of

trees infected in any one plot was 25. Of the 20 trees that were diagnosed with WPBR, 2 (10%) had stem cankers. The mean number of stem cankers per infected limber pine was 0.10 (Table 1.2) a value among the lowest of all study sites. On the other hand, the mean number of branch and stem cankers combined per infected limber pine at 10.4 was significantly higher than mean total cankers per infected limber pine at 8 of the 12 study sites with WPBR (Table 1.2). Dwarf mistletoe was very active in this area and was detected on 22.9% of evaluated limber pines, a higher proportion than at any of the other study sites. Bark beetles were evident on 73 (2.7%) of limber pines. Three of the trees infected with WPBR (15%) were also infected with dwarf mistletoe, and none had evidence of bark beetle attack. Of the dwarf mistletoe infected trees, 26 (4%) also had evidence of bark beetle attack. Of the declining and dying limber pines, only 0.9% were attributed to WPBR, 6% had been attacked by bark beetles, and 79% were attributed to dwarf mistletoe infections. Other damages recorded on the declining and dying limber pines were attributed to fire, wild animals, abiotic stresses, competition, and twig beetles. None of the recent dead limber pine had been killed by WPBR infection; 70% had evidence of bark beetle attack and 51% had evidence of dwarf mistletoe infestations.

Wind River

In the summer of 2004, 15 limber pine plots were established on the Wind River Indian Reservation. This area had the highest proportion of declining and dying trees of any of the 13 study sites with 33.6%; 61.4% of the limber pine where classified as healthy and 5.0% were dead. The elevational range of surveyed plots was 2,323 to 2,888 m. Sampled limber pines dominated stands that also had components of Douglas-fir in 60%

of plots, aspen in 47%, lodgepole pine in 27%, RM juniper in 20%, and subalpine fir in 13%. *Ribes* species recorded in the pine plots were *R. cereum* (60% of plots), *R. inerme* (13% of plots), and *R. lacustre* (1% of plots).

WPBR was present in every plot that was sampled in the Wind River Indian Reservation. This was the only study area for which that was true. The distribution of plots and their associated incidences of WPBR are displayed in Figure 1.17. Average incidence for the study area was 55.9%, which was significantly higher than that of any other study site (Table 1.1). The highest incidence in any single plot was 100% of the limber pine evaluated. Of the 290 limber pines that had cankers, 56 (19%) had stem cankers. The average number of stem cankers per infected limber pine was 0.22, and the mean number of branch and stem cankers combined per infected limber pine was 6.1 (Table 1.2). Dwarf mistletoe was recorded on 52 (9.4%) and bark beetles were recorded on 5 (0.9%) of evaluated limber pines. Of limber pines infected with WPBR, dwarf mistletoe was present on 23 (7.9%), and evidence of bark beetles was present on 2 (0.7%). No trees infected with dwarf mistletoe had evidence of bark beetle attack. Of the declining and dying limber pines, 43% were affected by WPBR, 17% by dwarf mistletoe infestations, and 1% by bark beetle attack. The remaining declining and dying limber pines had damages caused by defoliating insects, boring insects, wild animals, abiotic stresses, competition, and twig beetles. Of the recent dead limber pine, 75% had been killed by WPBR and 25% had evidence of bark beetle attack.

Relationships between WPBR incidence and tree and site variables

Diameter class was significantly related ($p<0.0001$) to likelihood of being infected by WPBR (Table 1.4). Trees greater than 15.3 cm DBH had a significantly greater likelihood of being infected by WPBR than limber pines in the smaller diameter classes. The mean number of cankers per tree also varied significantly by diameter class (Table 1.5), with the greatest average numbers of cankers on the largest diameter class trees (>30.5 cm), and significantly fewer cankers present on trees in each of the other diameter classes. Significantly fewer stem cankers, however, were present on trees greater than 30.5 cm DBH compared to limber pines in the smaller diameter classes. Among infected limber pines, trees > 30.5 cm DBH had an average of 10.5 cankers, compared to an average of 6.5 cankers on trees 15.3 – 30.5 cm, 4.0 cankers on 5.1 – 15.2, and 2.3 cankers on trees ≤ 5 cm.

Crown class, a description of an individual tree's position in the canopy relative to adjacent trees, was also significantly related to probability of infection by WPBR (Table 1.6). Trees in open and dominant/codominant crown classes had a significantly greater likelihood of being infected by WPBR than trees that were in intermediate or understory/overtopped crown classes. There were also significant differences in the average number of cankers per limber pine in the various crown classes (Table 1.7). Dominant trees had the highest average number of cankers at 2.1, followed by open and codominant trees with 1.1 and 1.0 cankers, respectively, and the fewest average number of cankers were present on trees in the intermediate, overtopped / understory crown classes (0.4 and 0.3, respectively). The average number of stem cankers was

significantly greater on open grown trees than on trees in the dominant, codominant and intermediate crown classes, but did not differ significantly from the average number of stem cankers on understory/overtopped trees. Among infected limber pines, there was a significant negative correlation between percent live crown and number of stem cankers ($r=-0.369$, $p<0.0001$).

Incidence of WPBR varied significantly by some plot variables. Incidence was significantly negatively correlated with elevation ($r=-0.412$, $p<0.0001$). Plots at elevations of less than 2590 m, of which 82% were found to be infested, had an average incidence of 23.5% (n=247) compared to the 257 plots located above 2590 m in which 30% of plots were infested and mean incidence was 7.7%, a statistically significant difference at $p<0.0001$. Incidence of WPBR was also positively correlated with geographic position, recorded in UTM coordinates, with more northerly ($r=0.346$, $p<0.0001$) and easterly ($r=0.262$, $p<0.0001$) plots having higher incidence of WPBR. Incidence varied significantly by slope position (Table 1.8) with those plots located near the bottom of slopes (valley bottom, toe slope, foot slope) having higher incidences of WPBR than plots located along slope shoulders and summits. There were no significant differences among plots with different classes of slope configuration. Plots on sites described as concave had a mean incidence of 23%, but that was not significantly different from the 16.7% mean incidence found on convex sites or 13.1% incidence on linear or even sites. Incidence did not vary significantly 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 (Figure 1.18).

Incidence did not vary significantly by canopy closure; stands described as having an open canopy had a mean incidence of 17.2% compared to 12.8% in stands described as having a closed canopy, but that difference was not statistically significant at p=0.05. White pine density was weakly negatively correlated with incidence (r=-0.092, p=0.04). There were significant differences in incidence related to dominant trees species presence. When ponderosa pine was one of the three dominant species on the plot, mean incidence was significantly greater (p=0.0075) at 19.0%, while plots with an absence of ponderosa pine had a mean incidence of 12.6% (Figure 1.19). Incidence of WPBR was significantly lower when lodgepole pine and subalpine fir were present (11.6% and 12.5%, respectively) as dominant species compared to plots where the lodgepole pine and subalpine fir were not dominant (20.0% (p<0.001) and 19.1% (p=0.02), respectively). Density of on-plot *R. cereum* was positively correlated to incidence of WPBR (r=0.157, p<0.0001), but there was no significant relationship between incidence of WPBR and density of the other species of *Ribes*. When *Artemisia tridentata*, big sagebrush, was present as one of the three dominant understory species mean incidence (n=221) was significantly higher (p=0.0017) at 12.6% compared to sites where big sagebrush was not a dominant understory cover (n=283), which had an average incidence of 5.1%. Mean incidence was also significantly higher (p=0.0036) at 15.0% on plots with *Symphoricarpos albus*, snowberry, present as a dominant understory component (n=27) compared to 2.8% on plots without snowberry as a dominant understory species (n=477).

Discussion

To our knowledge this is the first comprehensive, large-scale survey of limber pine health and WPBR to occur in central and southeastern Wyoming and northern Colorado. For the most part, limber pine throughout the surveyed area are healthy; however, WPBR is widespread and infecting 15.5% of evaluated limber pine within plots. A similar 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), by Smith and Hoffman (2000) found that WPBR was present on 59% of established plots and mean incidence within infected stands was 36%. These numbers are very similar to our findings of 55% of plots infected and average incidence within infected plots of 28%. However, 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. Among living whitebark pine trees in British Columbia, incidence was 38% with 66% of infected trees having potentially lethal stem cankers (Zeglen 2002). Campbell and Antos (2000) also surveyed whitebark pine stands in British Columbia and found that overall occurrence of the disease was higher (93% of 54 surveyed stands) and incidence was higher at 33% among surveyed stands compared to the mean incidence of 15.5% among surveyed plots reported here. Goheen et al. (2002) in a survey of whitebark pine along the Pacific Crest National Scenic Trail in Oregon reported that 46% of surveyed whitebark pines were alive and infected by *C. ribicola* and that 92% of the infected trees had stem cankers. Conklin (2004) working in New Mexico reported that 40% of southwestern white pines within established plots in the Sacramento Mountains were infected and 46% of infected white pines had stem cankers.

Recent surveys have found high levels of mortality, some of which is related to WPBR. Zeglen (2002) reported that 19% of examined whitebark pines in British Columbia were dead, of which 50% could be ascribed to WPBR. Campbell and Antos (2000) reported an overall level of mortality of 21.3% of their surveyed whitebark pines in British Columbia, of which 22% in young stands was attributed to WPBR but <5% of mortality in older stands were caused by WPBR. Goheen et al. (2002) reported that 10% of the whitebark pines surveyed in Oregon were dead. Smith and Hoffman (2000) reported that 8.7% of surveyed trees, including both limber and whitebark pines, were standing dead. Of the recently killed trees in that survey, 22% had evidence of WPBR stem cankers (Smith and Hoffman 2000). In New Mexico, the overall level of mortality in southwestern white pine was 2.8%, of which 70.6% was due to WPBR infection (Conklin 2004). The level of mortality in limber pine detected in this study averaged 5.0% on the 504 survey plots established and did not differ significantly between those plots with WPBR infected trees and those plots without WPBR. Of the recently killed limber pines in this study, 25.8% were infected by WPBR and 23.7% had stem cankers. This relatively low level of mortality compared to other studies in more northern areas may be a reflection of the shorter time of exposure to rust in these study areas, environmental conditions less suitable for pine infection, and genetic variation in both host susceptibility and pathogen virulence.

Differences among the 13 different study areas in terms of both disease incidence and severity are likely related to both the amount of time the pathogen has been present and to

differences in site suitability. WPBR incidence was greater in plots in northern locations where, presumably, the limber pine have been exposed to the pathogen for longer periods of time as it spread south and east from its introduction in British Columbia. Van Arsdel et al. (1998) report that the incidence of WPBR increased in the Sacramento Mountains of New Mexico with the length of time the pathogen had been present in the surrounding area. Conklin (2004) in reevaluating these plots found that the rate of increase in WPBR incidence averaged 2.6% per year.

To our knowledge this was the first report of WPBR in the Northern and Southern Snowy Range study sites, and the disease had only been detected in northern Colorado since 1998. While the disease did not appear to be having a significant ecological effect in the Northern and Southern Snowy Range and Roosevelt N.F. study sites, with 0.4, 0.9, and 1.1%, respectively, of declining and dying limber pines afflicted with WPBR at the time of this study, it is possible that the impact of WPBR on limber pines will increase over time in these areas. These areas likely represent the southern edge of the distribution of the pathogen as it continues to expand its distribution. Incidence was higher at the more northern locations, which is likely a reflection of the amount of time trees have been exposed to the pathogen in those areas. White pine blister rust is already altering forest composition through the selective removal of limber pines in some study areas. For example, 55% of the declining and dying limber pines at the Green Mountain study area were infected by *C. ribicola*, at the Laramie Peak East study site it was 49% of declining and dying and 72% of recent dead limber pine that were diseased. Scouting reports produced by USDA Forest Service employees from 1951 through 1969 never reported

the disease in the Green Mountain 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 site as early as 1969 (Brown 1978).

Four possible hypotheses are available for our inability to find the disease in the Sierra Madre study area. First, it is possible that spores of the pathogen have never been dispersed to this study area. However, it seems unlikely that the pathogen has never spread to the area due to its establishment in disjunct populations in southern Colorado (Blodgett and Sullivan 2004), New Mexico (Geils 2000, Van Arsdel et al. 1998), and South Dakota (Lundquist et al. 1992). The presence of the pathogen in the Sacramento Mountains of New Mexico, discovered in 1990 (Hawksworth 1990) and separate from other known infestation sites by 600 to 900 km, likely occurred through long-distance transport of aeciospores from the mountains of southern California (Geils 2000, Van Arsdel et al. 1998). At the time of the first report of WPBR in South Dakota, that infestation was isolated from the nearest known location of *C. ribicola* by 240 km and the nearest stand of limber pine by 160 km (Lundquist et al. 1992). Second, it is possible that while spores have been dispersed to the study area on air currents, the sites are so unconducive that the pathogen has never become established. This seems the most interesting of the explanations and requires further research. Determining which site factors present at the Sierra Madre might be detrimental to the establishment of *C. ribicola* could potentially provide much insight into the epidemiology and future distribution and impacts of the disease. Unfortunately, long-term meteorological data from this study site are nonexistent. Third, the pathogen may be present and established,

but our survey failed to locate any infected pines. To our knowledge no reports of WPBR on the Sierra Madre have been substantiated. Finally, it is possible that the pathogen has been dispersed throughout the Sierra Madre sites and that the conditions were suitable for spores to germinate and infections to occur, but that all of the limber pine in this study area possess some level of genetic resistance. Even though recent studies have indicated that major gene resistance may be present in populations of limber pine due to the expression of the hypersensitive reaction, no formal proof of major gene resistance in limber pine is currently available (Kinloch and Dupper 2002). Moreover, given that the frequencies of major resistance genes (Cr) in natural white pine populations are low - e.g., the average frequency of Cr1 in sugar pine is $\approx 2 \times 10^{-2}$ and for Cr2 in western white pine is between 10^{-3} and 10^{-4} (Kinloch 1992, Kinloch and Dupper 2002), it is highly unlikely that every limber pine in the Sierra Madre study area possesses a similar dominant gene for resistance to *C. ribicola*.

Relationships between WPBR and tree and site variables

Relationships between tree diameter and infection by WPBR similar to those found in this study have been reported by several authors. In the limber pine evaluated in this study, there was a significant increase in the number of branch and stem cankers with increasing diameter class, and trees greater than 15.3 cm DBH had a significantly greater probability of being cankered than small diameter trees. Campbell and Antos (2000) found that trees smaller than 10 cm DBH were half as likely to be infected as larger diameter whitebark pines. Conklin (2004) reported a higher proportion of infected southwestern white pines in larger diameter classes and higher occurrence of stem

cankers in trees in small diameter classes. Hunt (1983) reported increasing number of cankers with increased diameter in western white pine in British Columbia. 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 likely 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; although, this relationship was only significant for trees in the largest diameter class (>30.5 cm). 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, as 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. Trees in the dominant crown class had significantly greater numbers of branch and stem cankers. Limber pine in the open, dominant and codominant crown classes had a significantly higher probability of having 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 currents (i.e. spores may be

captured by the crowns overtopping and surrounding understory and intermediate trees). Campbell and Antos (2000) found that tree canopy cover was strongly related to incidence of WPBR in British Columbia with the highest infections levels found in stands with low canopy cover, i.e. stands comprised of open grown trees. Dahir and Cummings-Carlson (2001) also report that incidence of WPBR in Wisconsin on eastern white pine (*Pinus strobus* L.) was significantly lower in stands with a hardwood overstory, which they speculated served to trap spores preventing them from contacting the white pine understory.

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 (Van Arsdel et al. 1956). In general, *C. ribicola* is a fungus that prefers cool, moist conditions with temperatures for spore production and germination ranging from 1 to 24°C and requiring either the presence of free water or relative humidity in excess of 97% (Hirt 1942, Mielke 1943, Van Arsdel et al. 1956, Krebill 1971, McDonald et al. 1981). Krebill (1971) speculated that the reason the distribution of WPBR at the southern extent of its known range in the Rocky Mountains was observed to be limited to sites below 2440m elevation was due to low temperatures at higher elevations preventing production of basidiospores, the only spore stage that directly infects the pine host. In laboratory experiments he showed that basidiospores were produced at temperatures from 3 to 15°C, but only a few hundred basidiospores were cast at 3°C compared to several thousand cast at 15°C (Krebill 1971). Although there was a statistically significant relationship

between occurrence and incidence of WPBR and elevation, 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 to plots located above 2590 m (53%). However, they report that mean incidence was slightly higher in the plots located above 2590 m at 33% versus 31% on plots lower than 2590 m (Smith and Hoffman 2001). Conklin (2004) reports a strong positive correlation between elevation and incidence of WPBR in the Sacramento Mountains of New Mexico. Geils (2000) in the same area found higher occurrence, incidence, and severity of WPBR at elevations greater than 2400 m. 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 (Conklin 2004, Geils 2000). As the above studies illustrate, the relationship between incidence of WPBR and elevation is defined by the 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 *Ribes 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*. 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 to more mesic environments that support more susceptible species of *Ribes*. The relationship between species of *Ribes* and elevation may further influence incidence of WPBR and requires further study.

Kliejunas (1985) reported that incidence of WPBR in sugar pine (*Pinus lambertiana* Dougl.) in southern California was related to slope position. There, too, incidence declined from valley bottoms upslope to ridge tops (Kliejunus 1985). Cool air accumulates a the bases of slopes, which may super-cool leaves allowing dew to form providing the conditions necessary for basidiospores production and germination (Van Arsdel 1972). In the warmer regions of Wisconsin, where WPBR is relatively rare, pine infections are typically present at the bases of slopes (Van Arsdel 1972). However, the opposite was true in northern Wisconsin where incidence declined as one moved downslope: ridgetop trees had a mean incidence of 12.3%, midslope trees 7.6%, and bottomslope and flatland trees had a mean incidence of 5.4% (Dahir and Cummings-Carlson 2001). Even though the relationship between incidence and slope position is

statistically significant in this study, this variable's utility in predicting incidence in unsurveyed areas may be limited.

Conclusions

Krebill (1964) reported that spread of WPBR through high elevation white pine stands in the central Rocky Mountains appeared to be slow, but cautioned readers 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 campground in the Pole Mountain study area, are currently being heavily impacted by the rust and mortality of mature trees is occurring. Other areas, such as the Northern Snowy Range, appear to be less impacted with very few trees infected by the pathogen. While the majority of limber pines surveyed for this study were healthy, WPBR was infecting 14% of evaluated trees. This level of infestation has been attained within the past two to four decades, and with time the pathogen may spread to currently uninfested white pine populations and intensify throughout its current distribution. Monitoring of permanent 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. In addition to directly killing mature trees, white pine blister rust 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). The native white pine populations that occupy high elevation sites throughout the central and southern Rocky Mountains contribute many valuable ecological and social values. There is a clear need to evaluate the roles and interactions of the pine and alternate hosts, microclimatic conditions, and time in order to aid the monitoring of this invasive, non-native pathogen and its effects on these important ecosystems.

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Figure 1.1. White pine blister rust study areas in Wyoming and northern Colorado

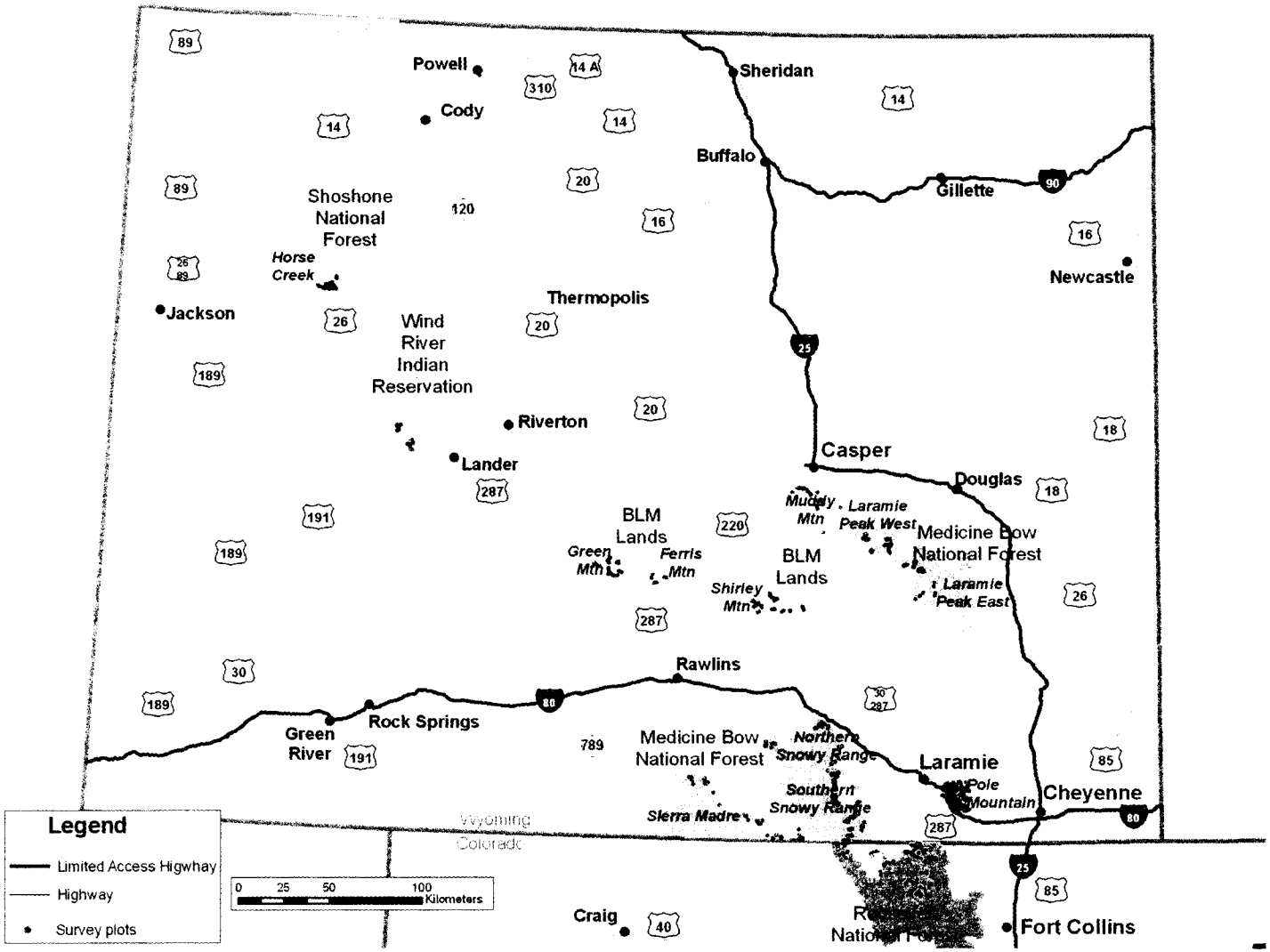
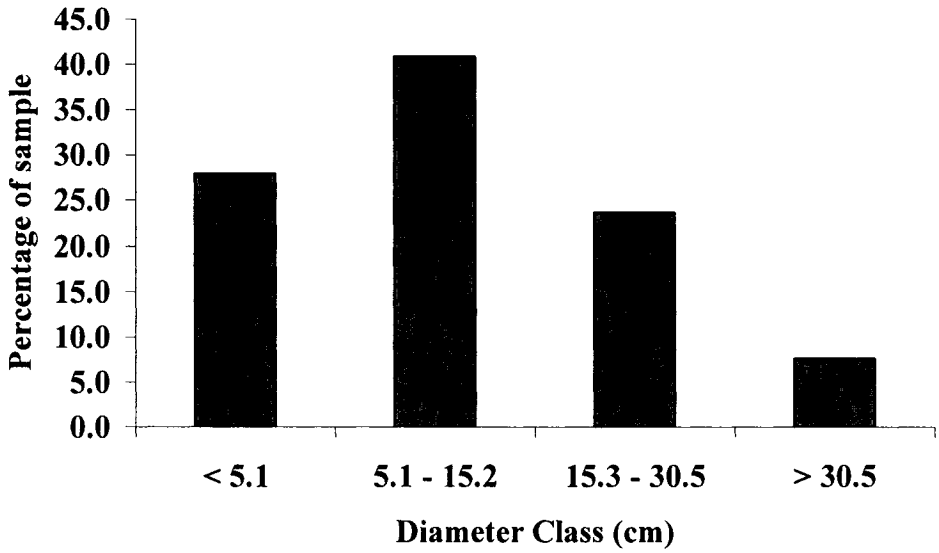
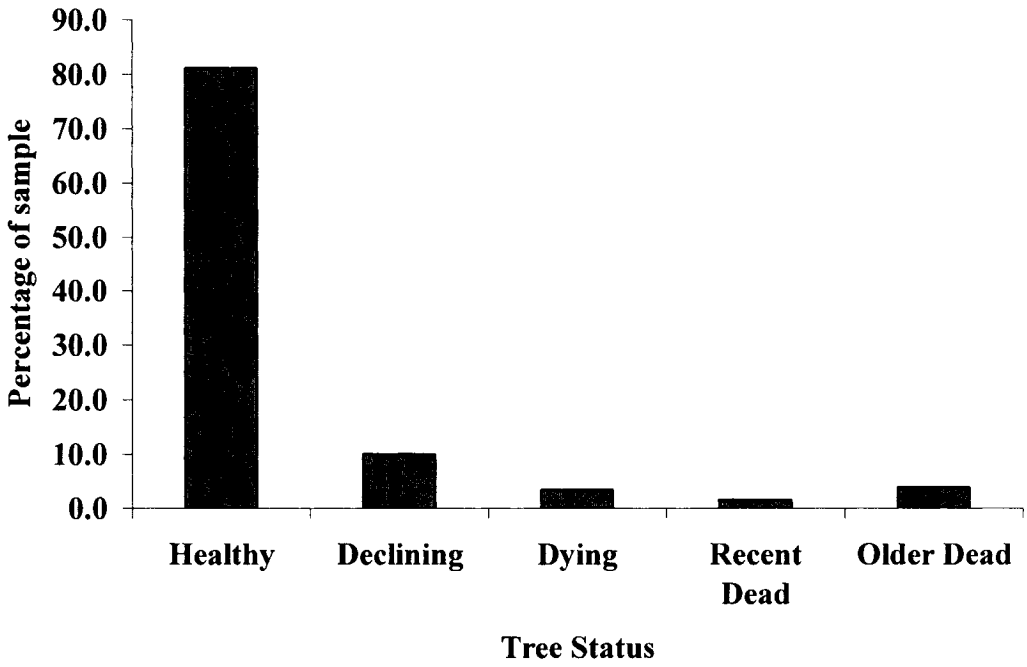


Figure 1.2. Limber pine diameter class distribution[1]



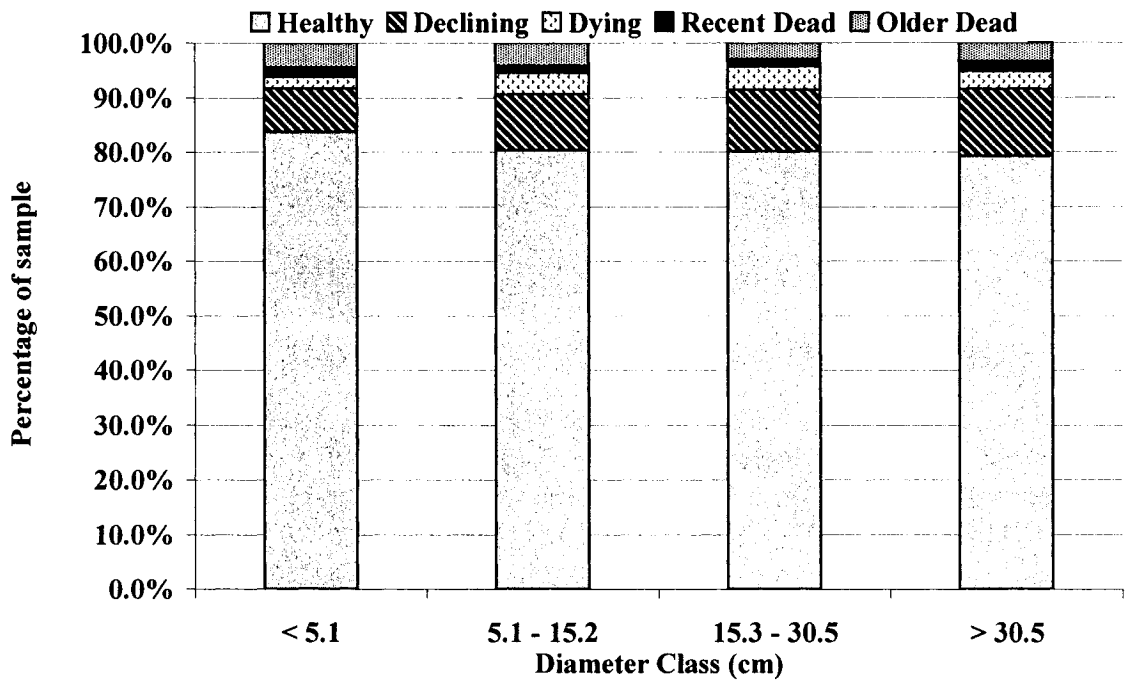
[1] Sample size = 18,719 limber pine >1.37 m

Figure 1.3. Limber pine status[1]



[1] Sample size = 18,719 limber pine >1.37 m

Figure 1.4. Limber pine status by diameter class[1]



[1] Sample size = 18,719 limber pine >1.37 m; <5.1cm DBH (n=5229), 5.1 – 15.2 cm DBH (n=7647), 15.3 – 30.5 cm DBH (n=4423), >30.5 cm DBH (n=1420).

Figure 1.5. Location of plots and their associated incidence of WPBR - Ferris Mountain, Wyoming.

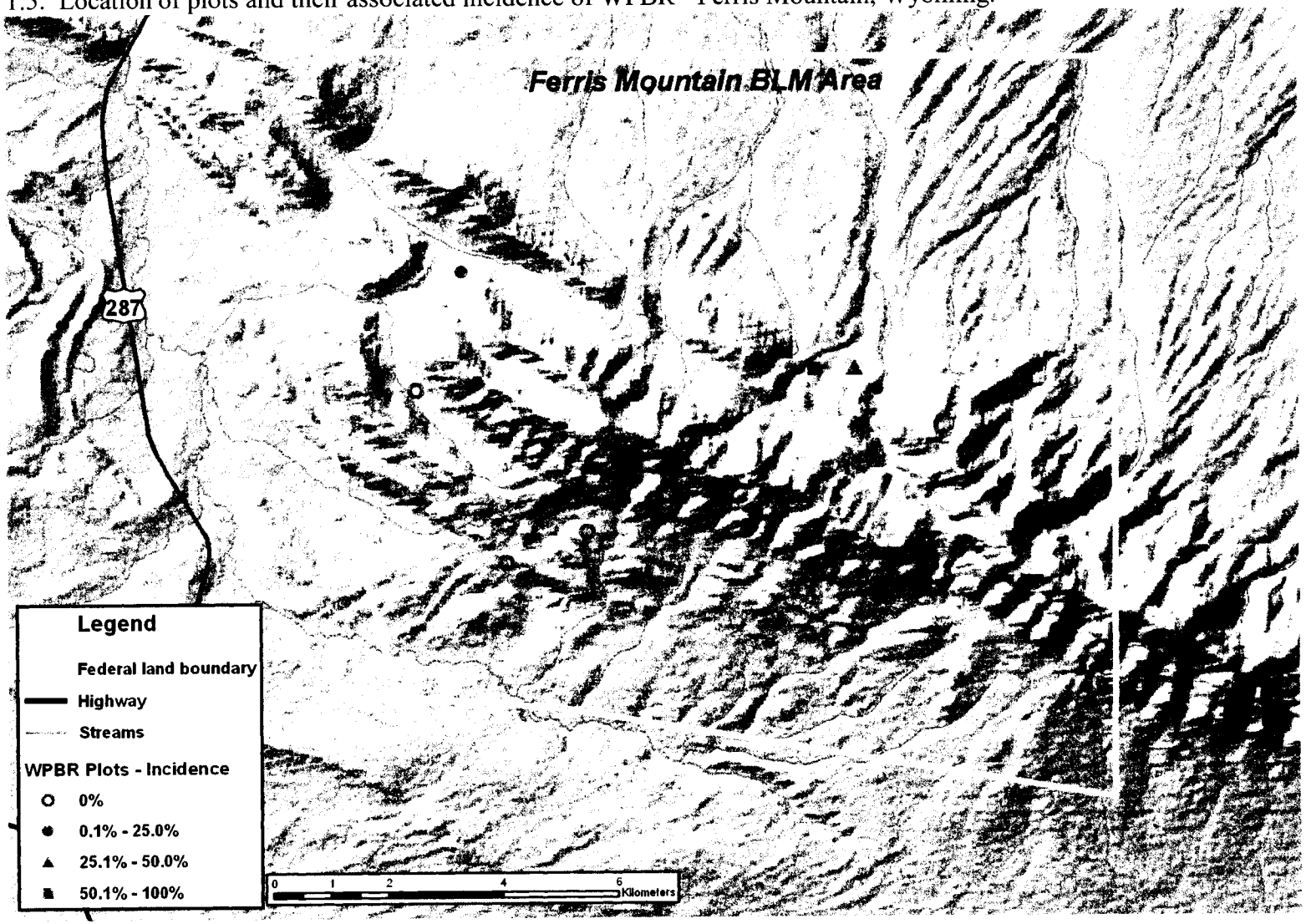


Figure 1.6. Distribution of plots and their associated incidences of WPBR - Green Mountain, Wyoming.

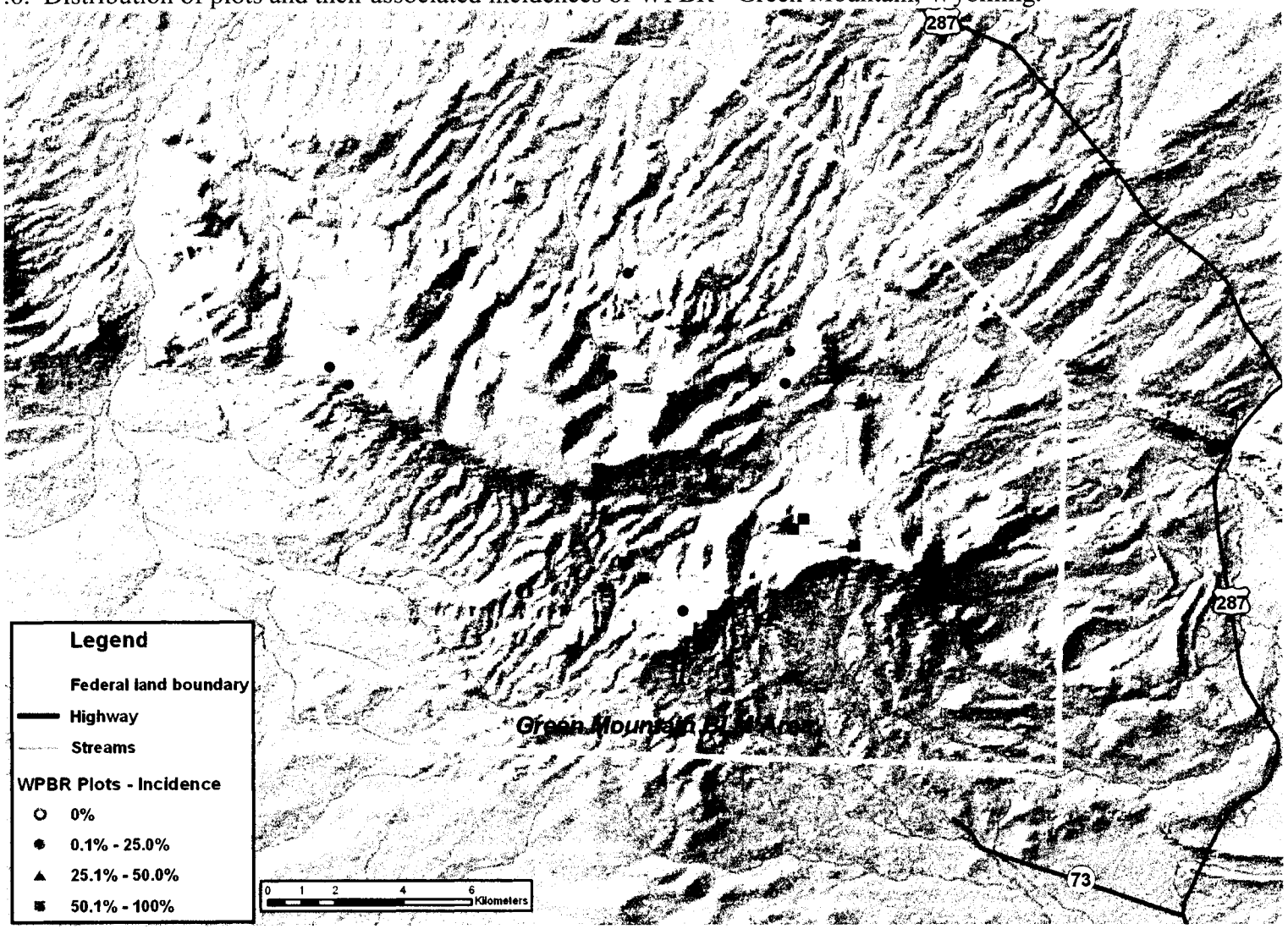


Figure 1.7. Distribution of plots and their associated incidences of WPBR – Horse Creek, Shoshone National Forest, Wyoming.

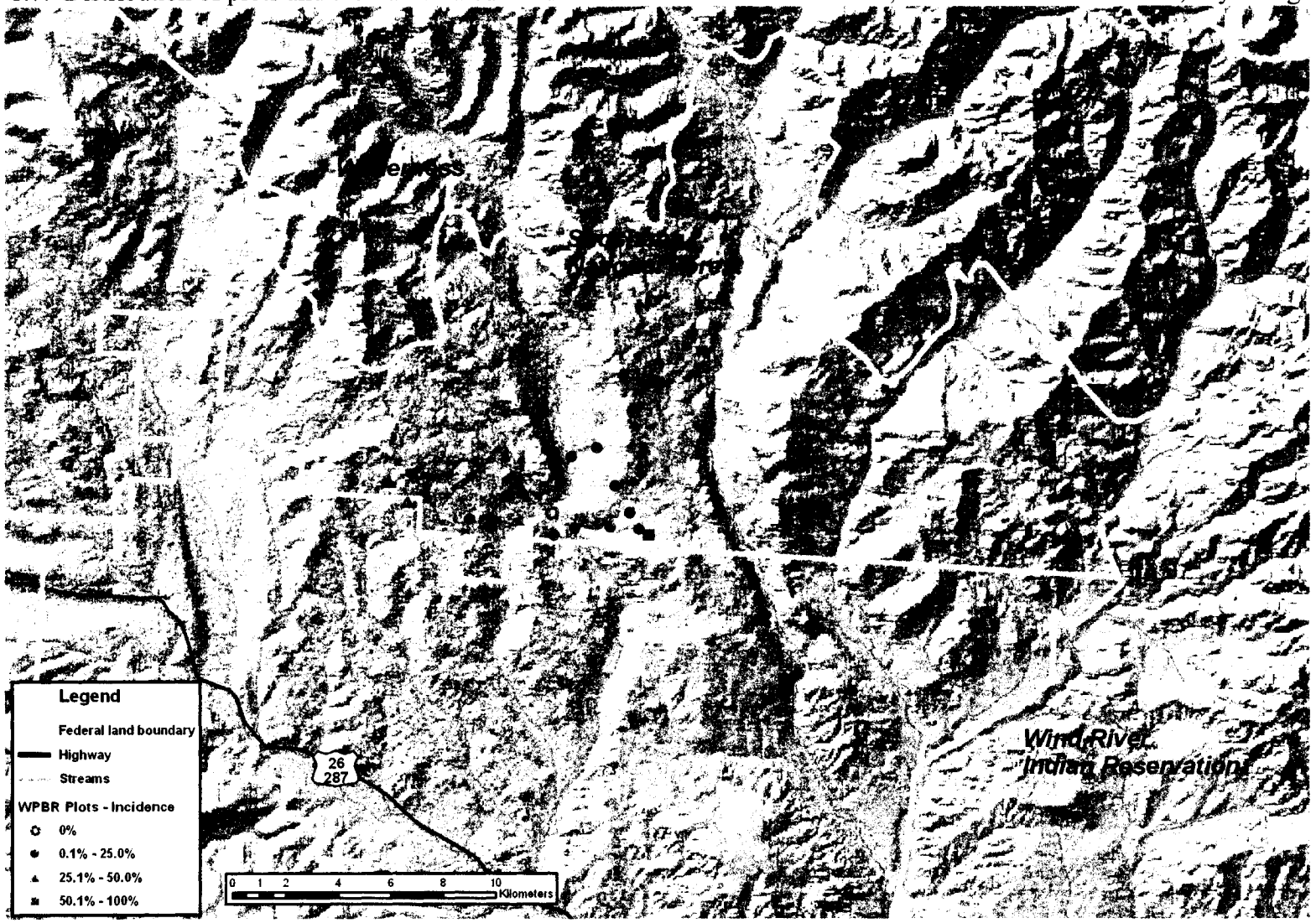


Figure 1.8. Distribution of plots and their associated incidences of WPBR - Laramie Peak East, Medicine Bow National Forest, Wyoming.

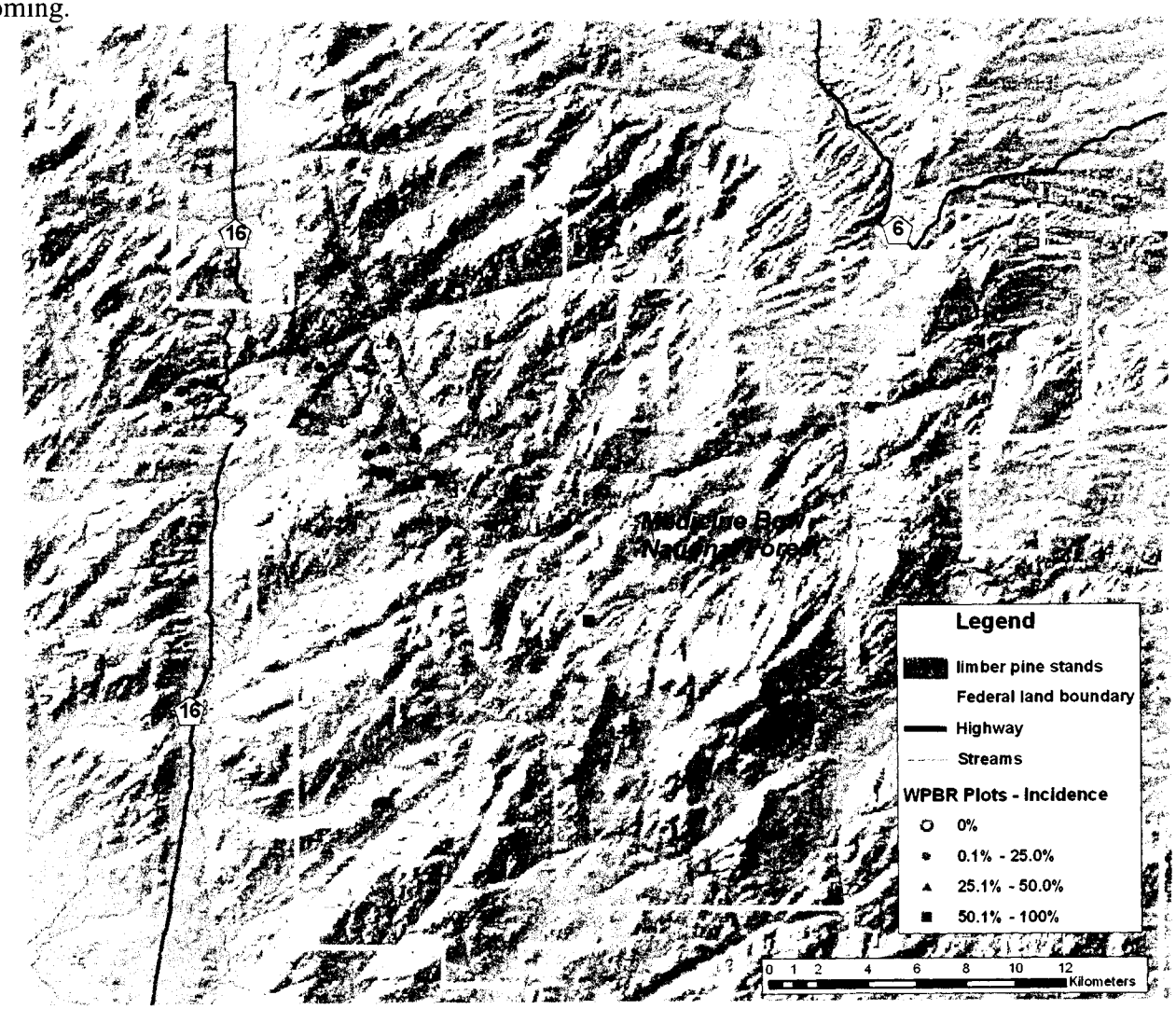


Figure 1.9. Distribution of plots and their associated incidences of WPBR - Laramie Peak West, Medicine Bow National Forest, Wyoming.

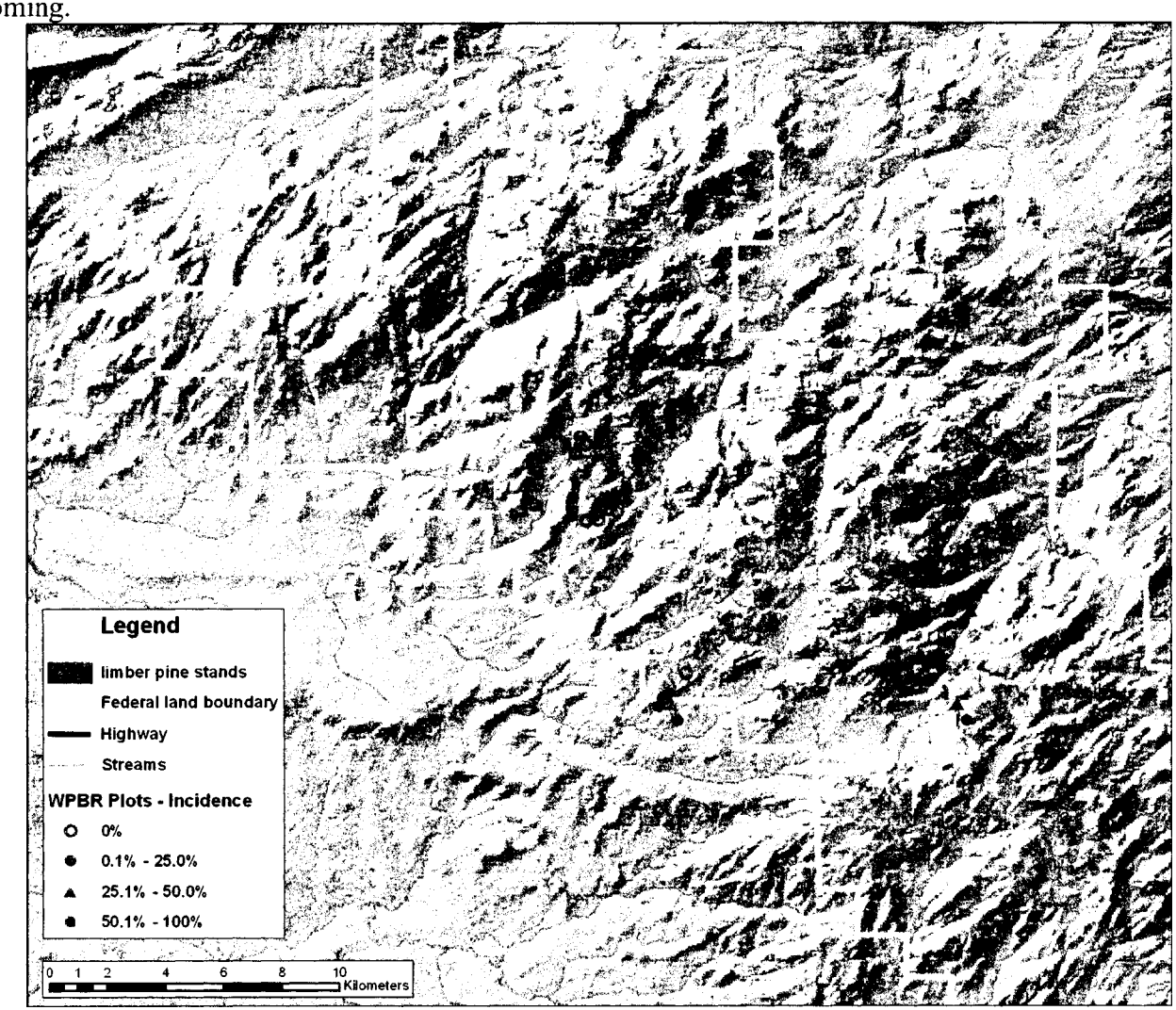


Figure 1.10. Distribution of plots and their associated incidences of WPBR - Muddy Mountain, Wyoming.

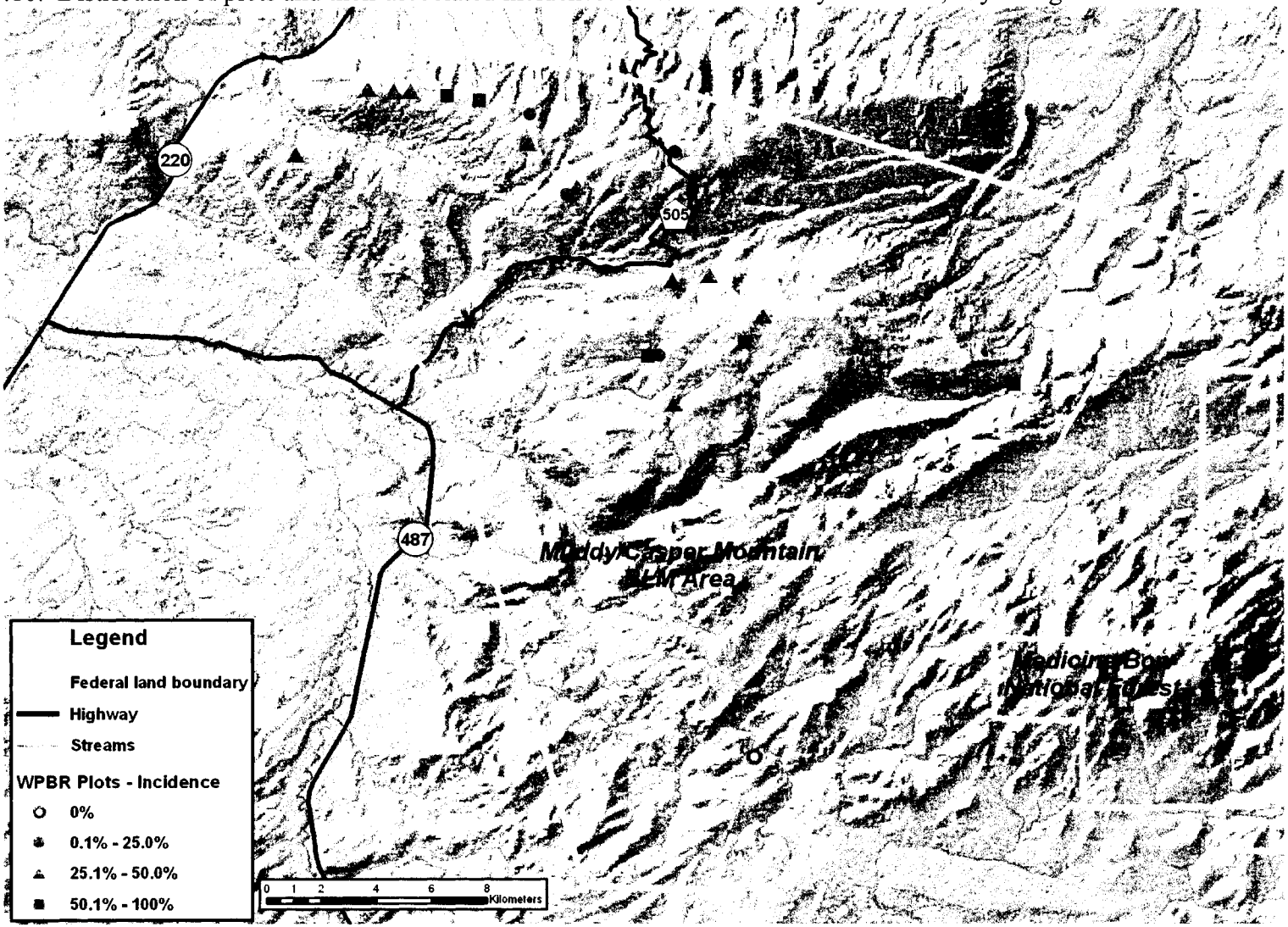


Figure 1.11. Distribution of plots and their associated incidences of WPBR - Northern Snowy Range, Medicine Bow National Forest, Wyoming.

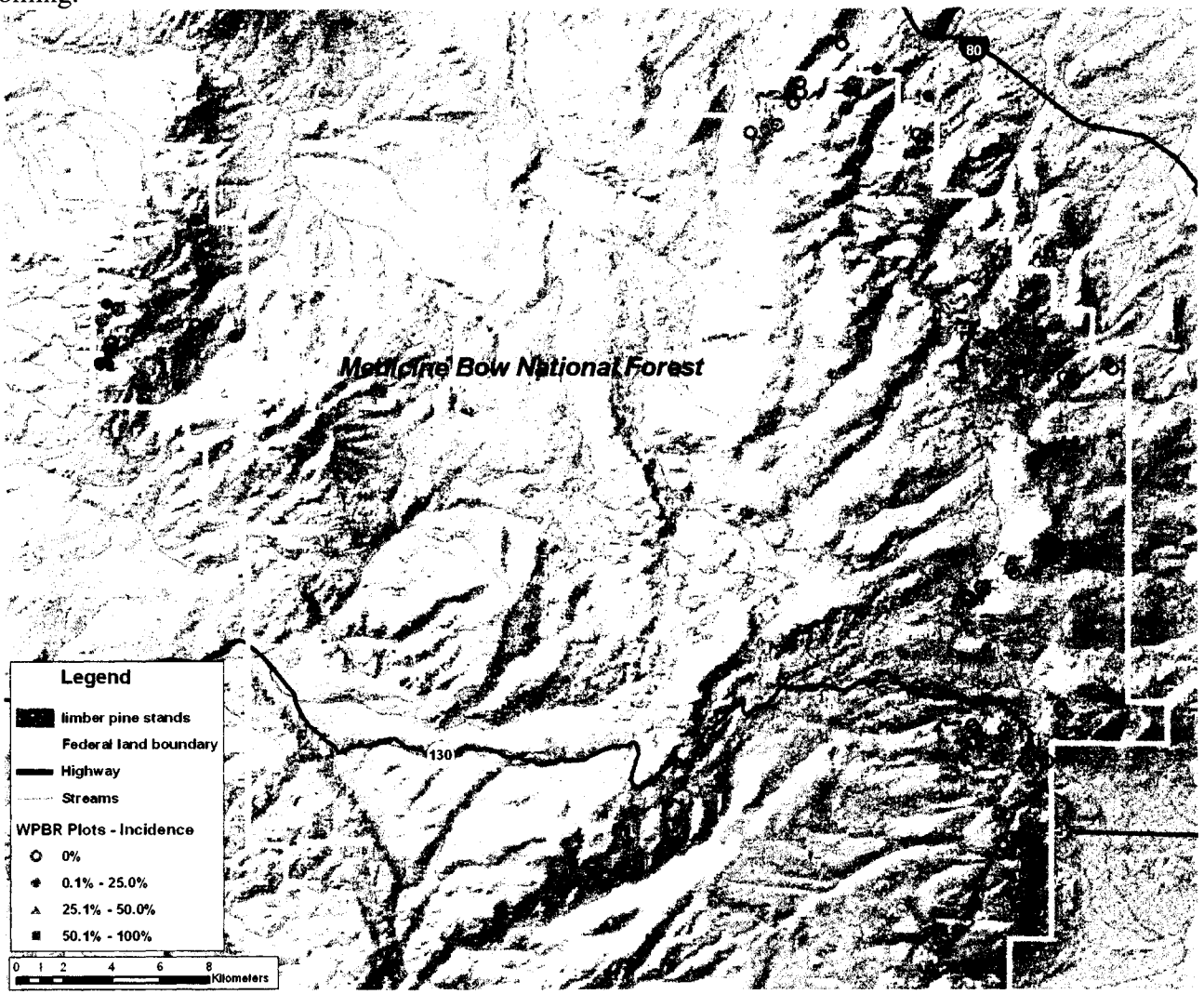


Figure 1.12. Distribution of plots and their associated incidences of WPBR - Pole Mountain, Medicine Bow National Forest, Wyoming.

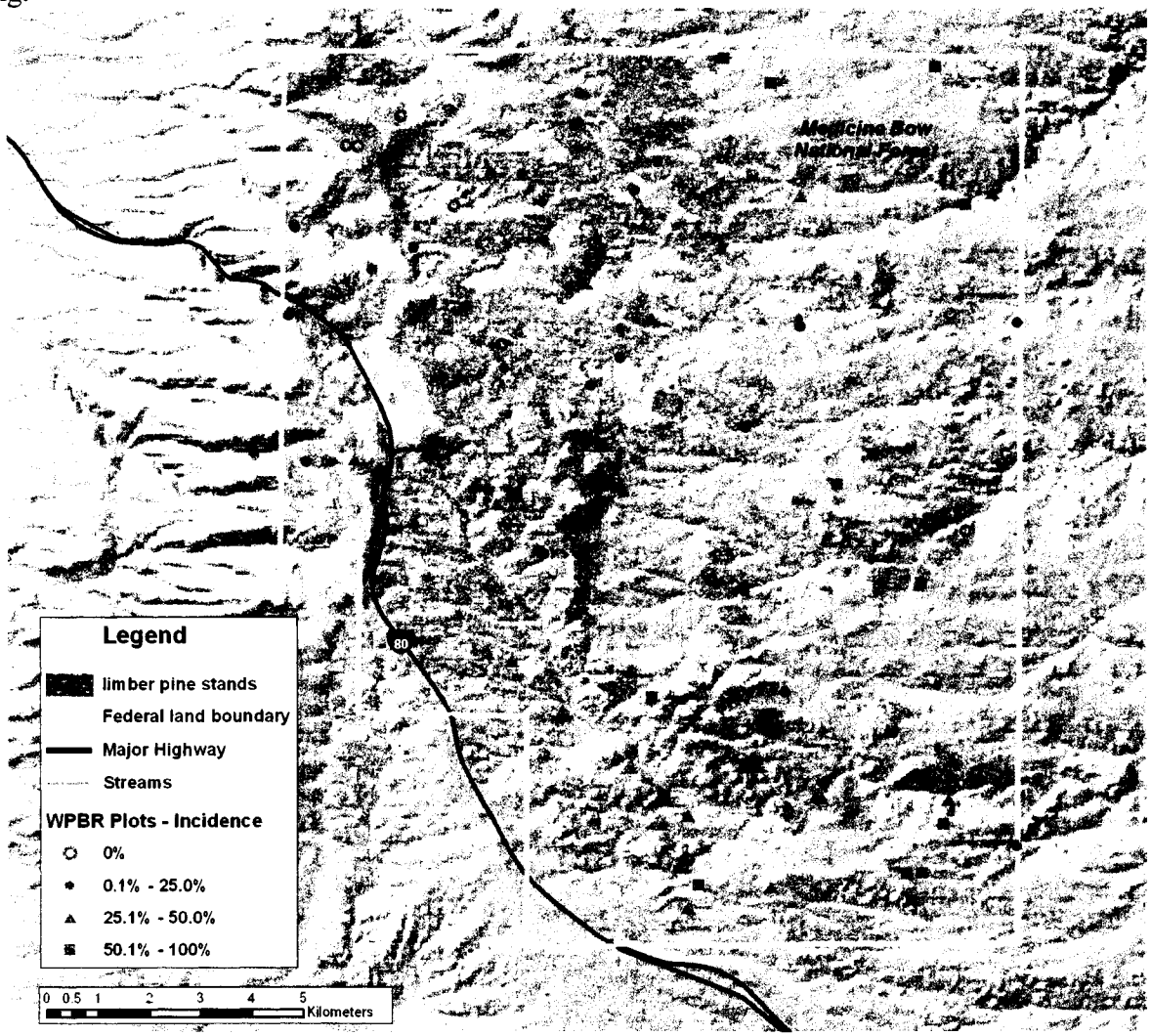


Figure 1.13. Distribution of plots and their associated incidences of WPBR - Roosevelt National Forest, Colorado.

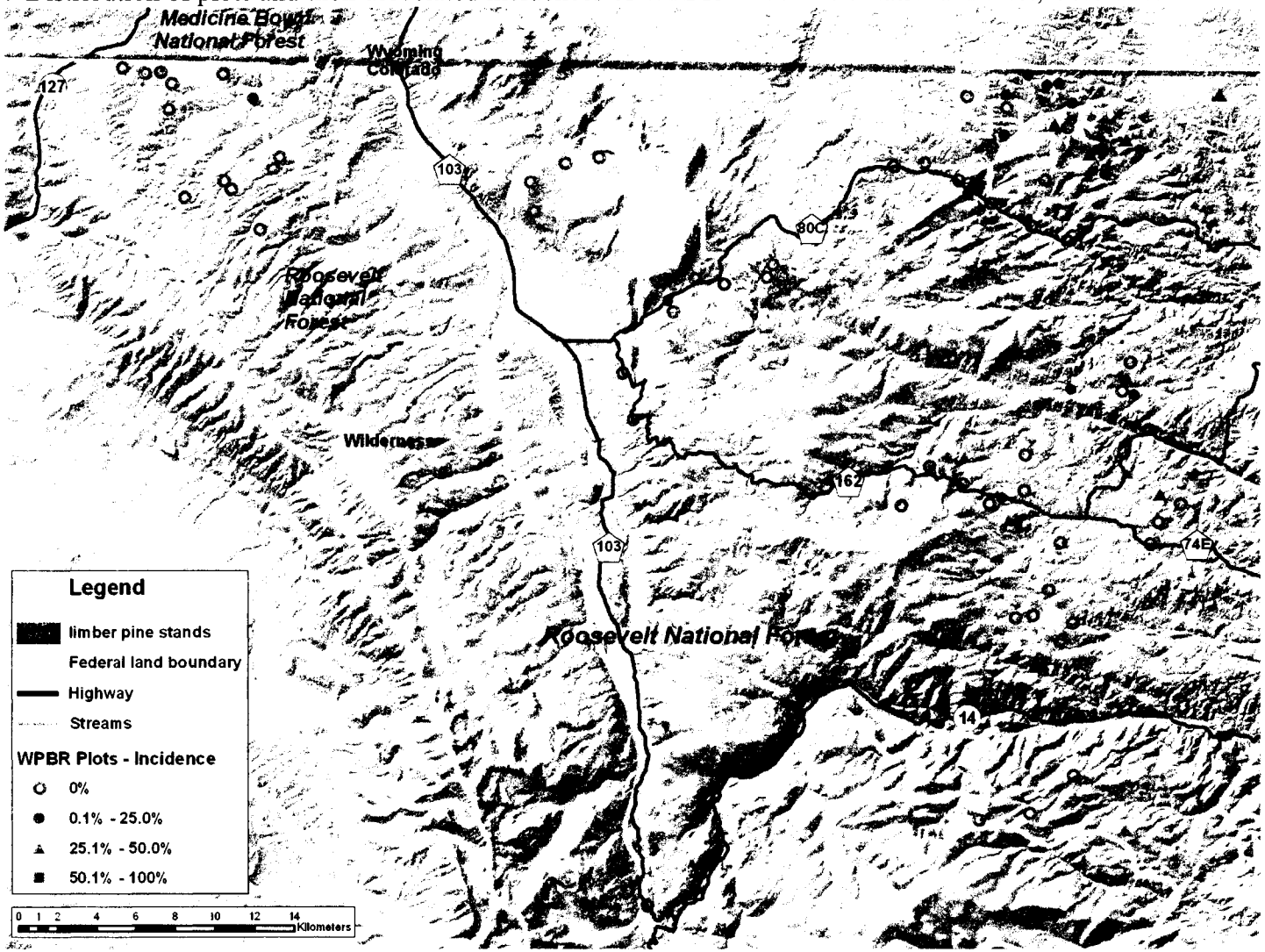


Figure 1.14. Distribution of plots and their associated incidences of WPBR - Shirley Mountains, Wyoming.

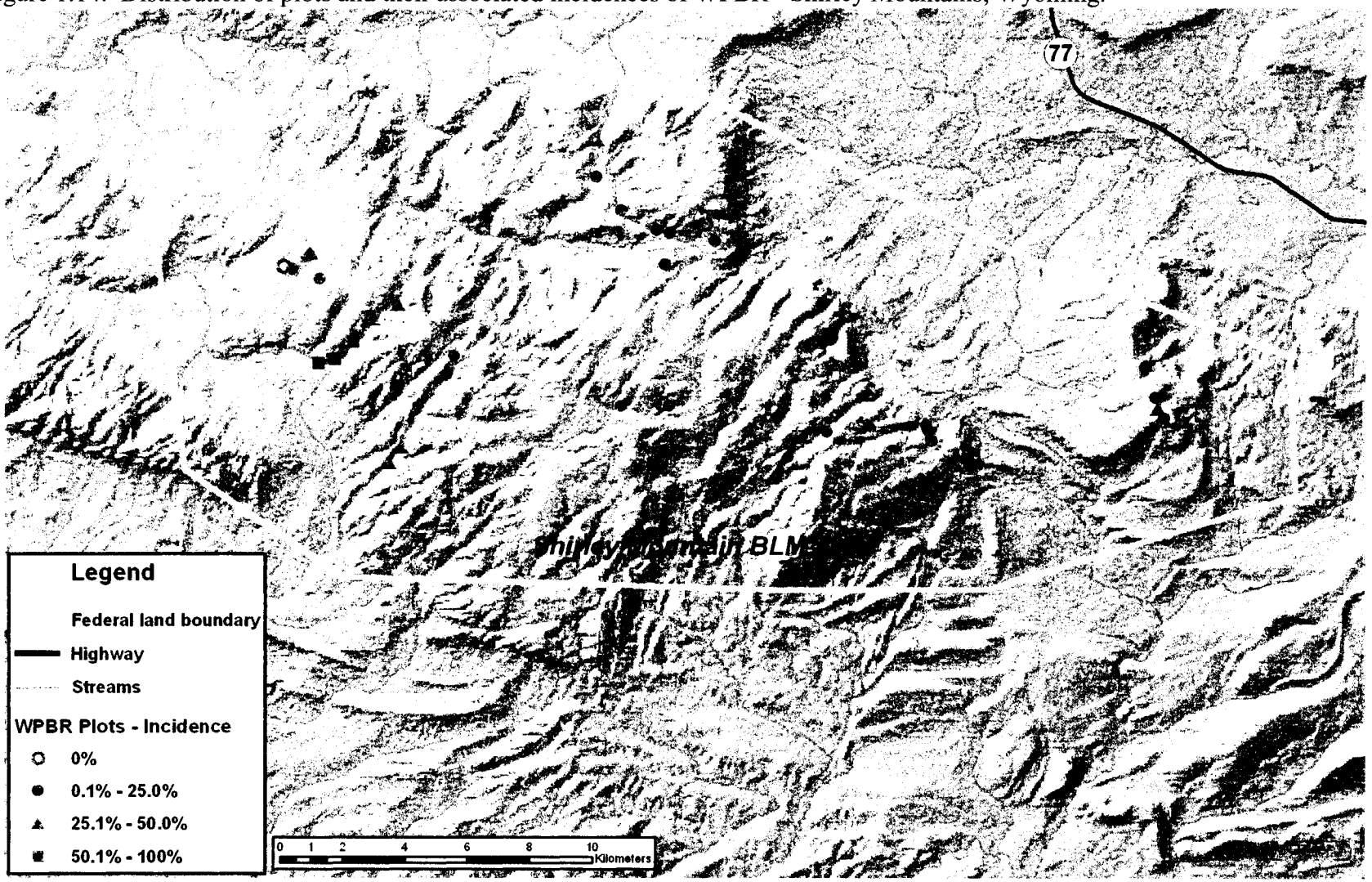


Figure 1.15. Distribution of plots and their associated incidences of WPBR - Sierra Madre, Medicine Bow National Forest, Wyoming.

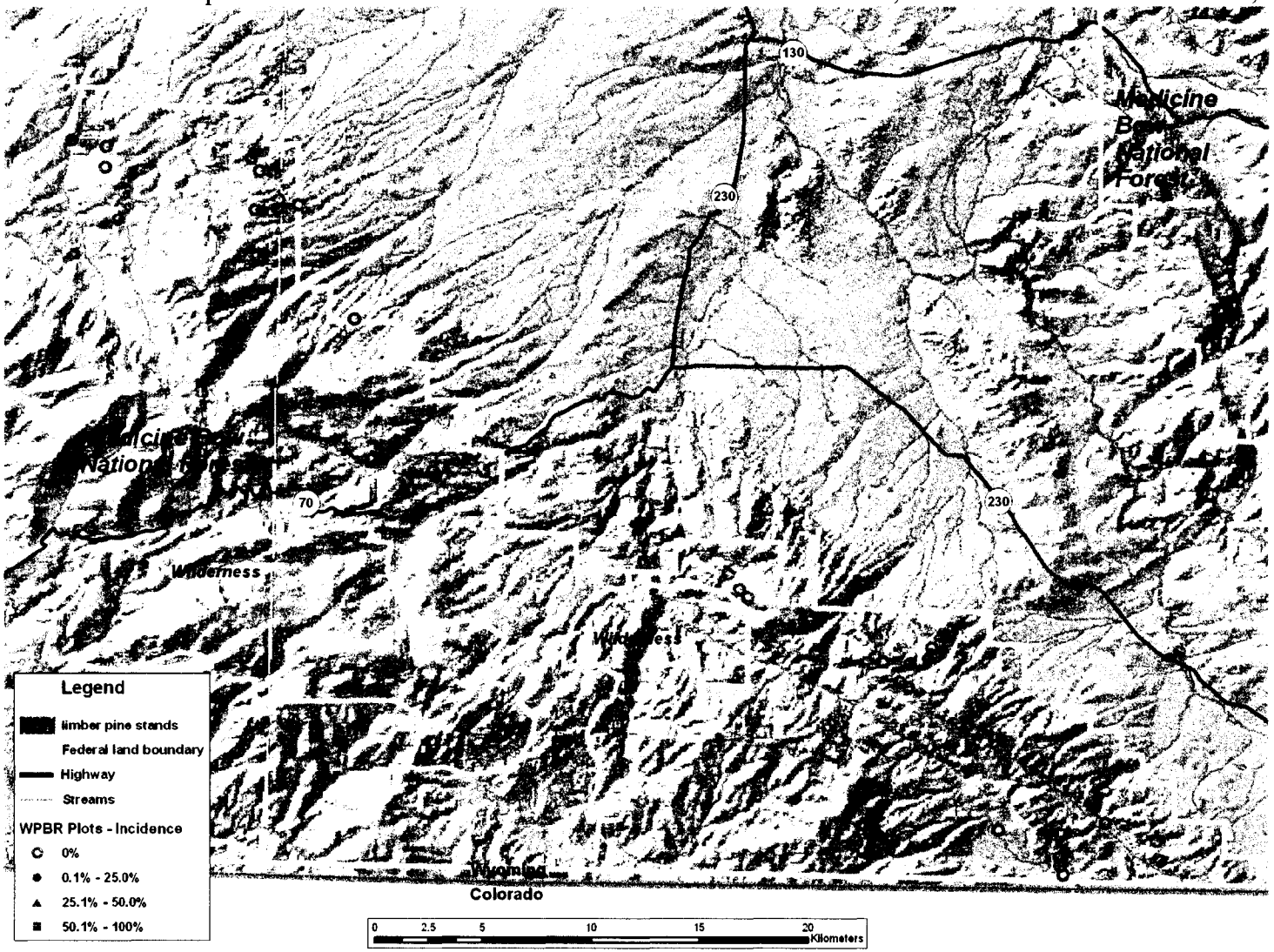


Figure 1.16. Distribution of plots and their associated incidences of WPBR - Southern Snowy Range, Medicine Bow National Forest, Wyoming.

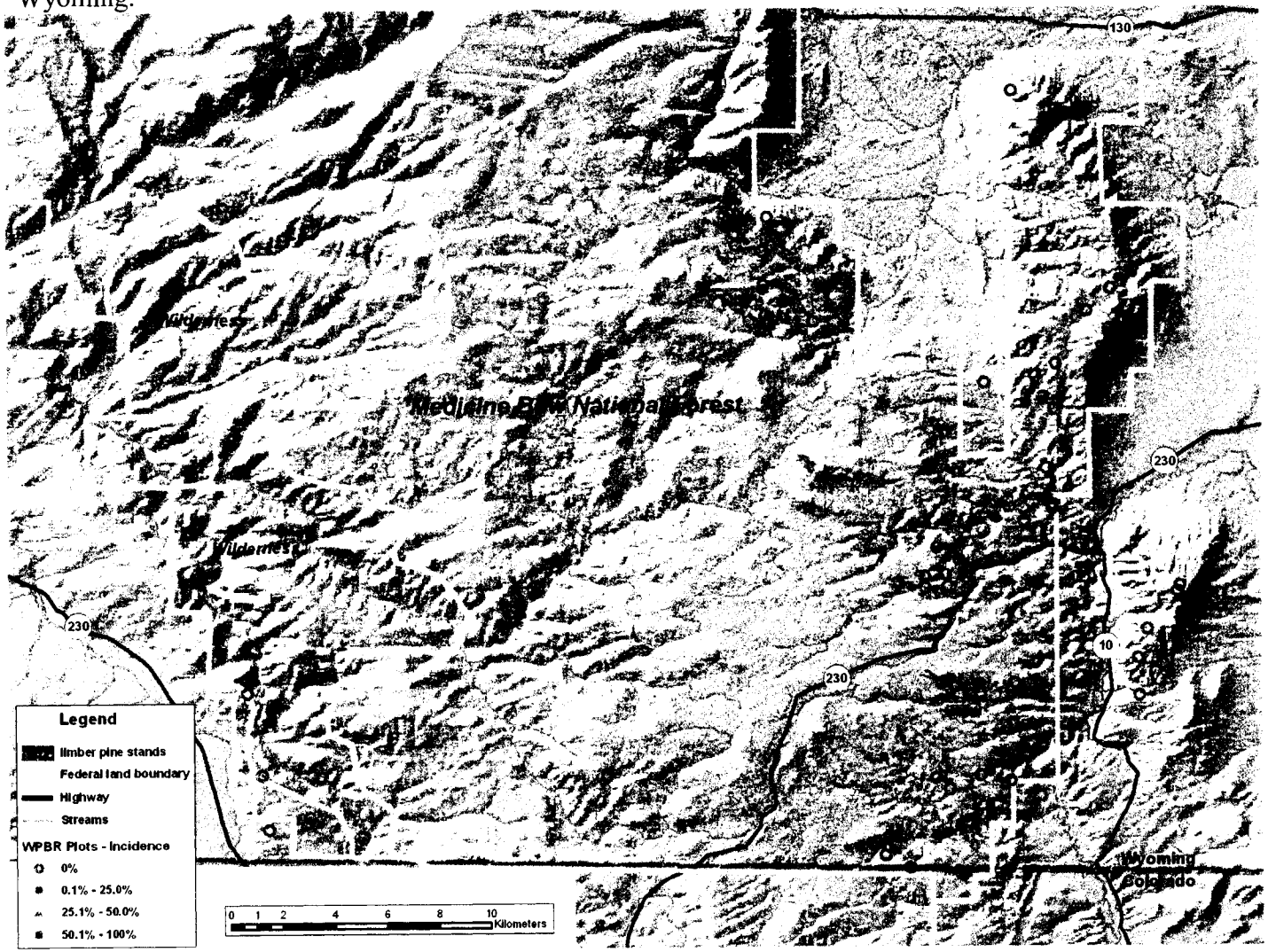


Figure 1.17. Distribution of plots and their associated incidences of WPBR - Wind River Indian Reservation, Wyoming.

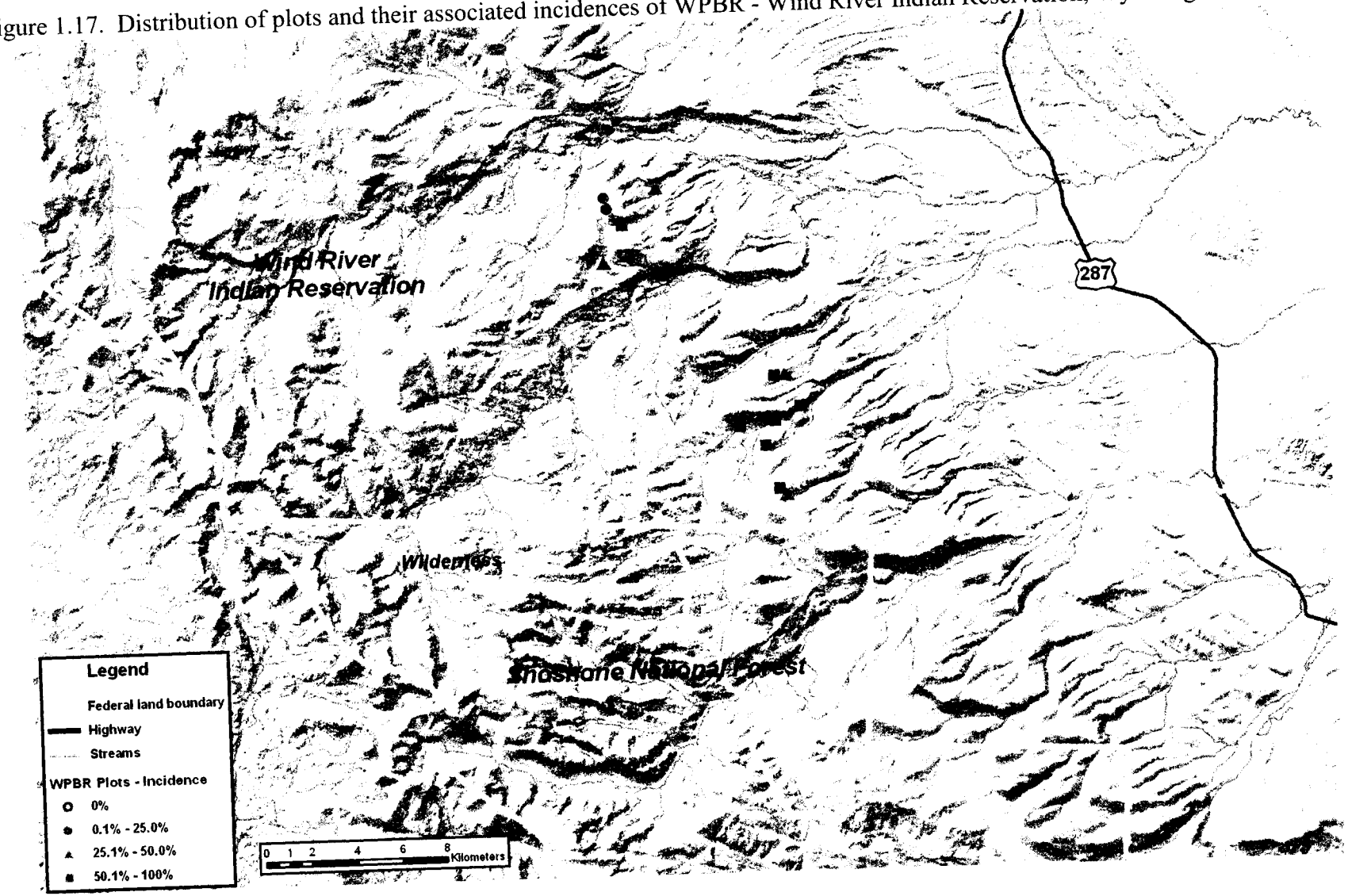
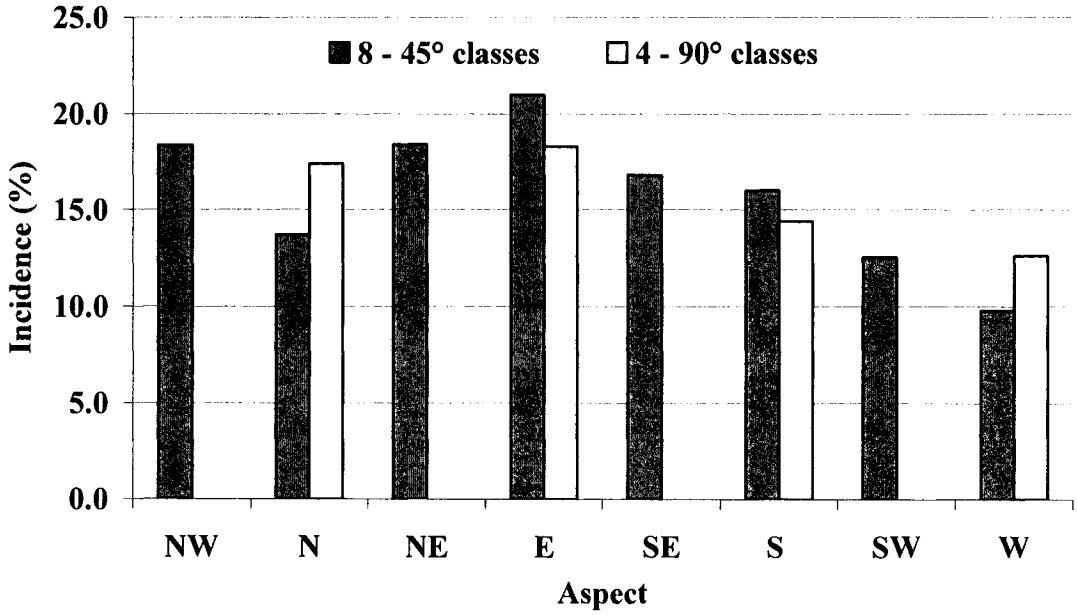
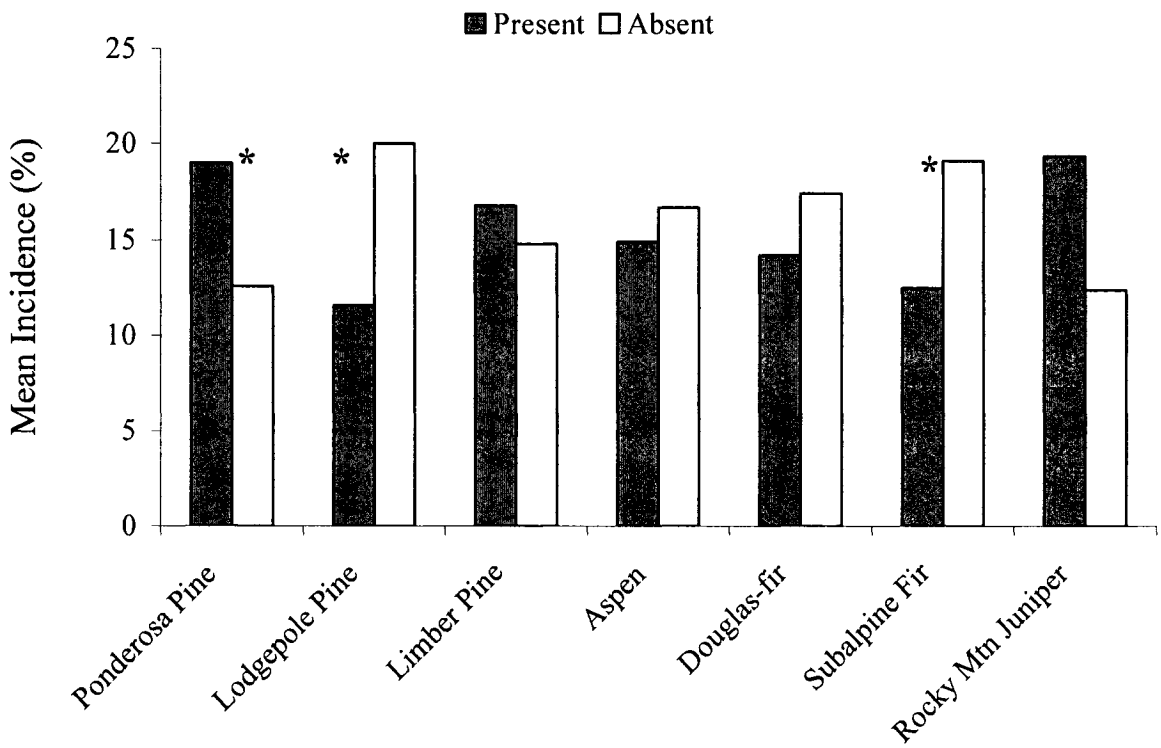


Figure 1.18. Incidence of white pine blister rust on limber pine by plot aspect class.



[1] 45°aspect classes (NE 22.5-67.5° (n=45), E 67.5-112.5° (n=47), SE 112.5-157.5° (n=62), S 157.5-202.5° (n=56), SW 202.5-247.5° (n=65), W 247.5-292.5° (n=69), NW 292.5-337.5° (n=74), N >337.5° and <22.5° (n=86)). 90° aspect classes (N >314.5° and <45° (n=143), E 45-134° (n=96), S 135-224° (n=118), and W 225-314 (n=147)).

Figure 1.19. Incidence of white pine blister rust on limber pine by presence of dominant tree species[1].



[1] Tree species as one of the 3 dominant tree species on the plot

* Differences between presence/absence within species are significant at p=0.05 based on paired t-test.

Table 1.1. Incidence of white pine blister rust at 13 study areas in Wyoming and northern Colorado.

Site	N[1]	Incidence[2]	S. D.[3]	Range	Tukey[4]
Wind River	15	55.9	23.2	19.5 – 100	a
Muddy Mountain	20	37.1	20.5	0 – 72.7	b
Green Mountain	22	35.7	24.4	2.8 – 75.8	bc
Pole Mountain	93	30.4	22.3	0 – 76.5	bcd
Laramie Peak East	29	27.2	20.4	0 – 91.7	bcd
Ferris Mountain	7	21.6	29.8	0 – 76.9	cd
Shirley Mountains	33	19.7	19.0	0 – 72.4	de
Horse Creek, SNF	20	18.6	12.8	0 – 52.9	def
Laramie Peak West	30	6.6	9.0	0 – 28.6	efg
Roosevelt NF	75	4.1	9.6	0 – 47.1	fg
Northern Snowy	60	1.2	2.9	0 – 12.8	g
Southern Snowy	69	0.9	3.9	0 – 25.0	g
Sierra Madre	31	0.0	0	0	g
Total	504	15.5	21.4	0 – 100	

[1] The number of plots established within each study site.
[2] Incidence is the number of infected trees/number of evaluated trees averaged over all plots established in the study site.
[3] Standard deviation.
[4] Values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 1.2. White pine blister rust branch and stem cankers in Wyoming and northern Colorado.

		Total Cankers[1]			Stem Cankers[2]		
Site	N[3]	Mean	S. D.[4]	Tukey[5]	Mean	S. D.[4]	Tukey[5]
Southern Snowy	20	10.4	23	a	0.10	0.31	c
Green Mountain	295	7.6	15.1	ab	0.20	0.57	bc
Pole Mountain	801	6.8	10.8	abc	0.32	0.60	abc
Wind River	290	6.1	9.2	abcd	0.22	0.48	bc
Ferris Mountain	90	4.3	4.9	bcd	0.53	0.74	a
Shirley Mountains	274	3.2	4.4	bcd	0.44	0.58	ab
Muddy Mountain	223	3.1	3.8	bcd	0.17	0.40	bc
Roosevelt NF	83	2.7	2.9	cd	0.08	0.28	c
Laramie Peak East	258	2.7	3.7	cd	0.53	0.63	a
Laramie Peak West	65	2.2	2.4	cd	0.34	0.54	abc
Horse Creek, SNF	133	2.0	1.4	d	0.09	0.31	c
Northern Snowy	32	1.6	1.3	d	0.16	0.37	bc
Sierra Madre	0	0.0	0	n/a	0.00	0.00	n/a

[1] Mean number of branch and stem cankers per infected limber pine.
[2] Mean number of stem cankers per infected limber pine.
[3] Number of WPBR infected trees evaluated within each study site.
[4] Standard deviation.
[5] Values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 1.3. Relationships between white pine blister rust, dwarf mistletoe, and bark beetles.

	WPBR Present Dwarf Mistletoe[1]					WPBR Absent Dwarf Mistletoe				
Bark Beetles	None	Mild	Mod.	Severe	Row Total	None	Mild	Mod.	Severe	Row Total
BB Present (#)	29	0	0	0	29	108	2	17	25	152
BB Present %	1.1	0.0	0.0	0.0	1.1%	0.7	0.0	0.1	0.2	1.0%
BB Absent (#)	2410	71	32	22	2535	13830	470	450	521	15271
BB Absent %	94.0	2.8	1.3	0.9	98.9%	89.7	3.1	2.9	3.4	99.0%
DM %	95.1%	2.8%	1.2%	0.9%		90.4%	3.1%	3.0%	3.5%	

[1] DMR (Dwarf Mistletoe Rating)1 and 2 = Mild, DMR 3 and 4 = Moderate, DMR 5 and 6 = Severe.

Table 1.4. Probability of white pine blister rust canker presence by diameter class.

Diameter Class (cm)	N[1]	Probability of cankers[2]	
>30.5	1371	0.19	a
15.3 – 30.5	4290	0.18	a
5.1 – 15.2	7331	0.14	b
< 5	4995	0.11	c

[1] Number of limber pine sampled.
[2] Values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 1.5. Mean number of white pine blister rust cankers and stem cankers by diameter class.

Diameter Class (cm)	N[1]	Total Cankers[2]	Stem Cankers[3]
> 30.5	1371	2.0 a	0.02 b
15.3 - 30.5	4290	1.2 b	0.05 a
5.1 - 15.2	7331	0.6 c	0.04 a
≤ 5	4995	0.2 d	0.04 a

[1] Number of limber pine sampled by diameter class.
[2] Mean number of branch and stem cankers combined, values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.
[3] Mean number of stem cankers, values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 1.6. Probability of white pine blister rust canker presence by crown class.

Crown Class	N[1]	Probability of cankers[2]	
Open	2851	0.16	a
Dominant / Codominant	6153	0.16	a
Intermediate	5433	0.13	b
Understory / Overtopped	3434	0.11	c

[1] Number of limber pine sampled by crown class.
[2] Values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 1.7. Mean number of white pine blister rust cankers and stem cankers by crown class.

Crown Class	N[1]	Total Cankers[2]	Stem Cankers[3]
Dominant	420	2.1 a	0.03 b
Open	2851	1.1 b	0.06 a
Codominant	5733	1.0 b	0.04 b
Intermediate	5433	0.4 c	0.04 b
Overtopped / Understory	3434	0.3 c	0.05 ab

[1] Number of limber pine sampled by crown class.
[2] Mean number of branch and stem cankers combined, values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.
[3] Mean number of stem cankers, values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 1.8. Mean incidence of white pine blister rust by slope position.

Slope Position	N[1]	Incidence[2]	
Valley Bottom	15	29.7	a
Toe Slope	24	24.7	ab
Foot Slope	44	23.2	abc
Back Slope	195	16.2	abc
Ridge / Summit	100	12.7	bc
Shoulder	126	10.2	c

[1] Number of plots established in each slope position category.
[2] Mean incidence, values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Appendix 1.1. Location of survey plots

		UTM Coordinates		
Study Area	**Plot #**	**Zone**	**Easting (m)**	**Northing (m)**
Ferris Mtn	FM 1801	13	302947	4687117
Ferris Mtn	FM 1802	13	309796	4685401
Ferris Mtn	FM 1803	13	310188	4685018
Ferris Mtn	FM 1804	13	309091	4685369
Ferris Mtn	FM 1805	13	303706	4681984
Ferris Mtn	FM 1806	13	305115	4682524
Ferris Mtn	FM 1807	13	302132	4685028
Green Mtn	GM 5001	13	283809	4686164
Green Mtn	GM 5002	13	278653	4690461
Green Mtn	GM 5003	13	279428	4687692
Green Mtn	GM 5004	13	279001	4688948
Green Mtn	GM 5005	13	278858	4693744
Green Mtn	GM 5006	13	270817	4693500
Green Mtn	GM 5007	13	271381	4693004
Green Mtn	GM 5008	13	272452	4692346
Green Mtn	GM 5009	13	274111	4691195
Green Mtn	GM 5010	13	279088	4693273
Green Mtn	GM 5011	13	279569	4696271
Green Mtn	GM 5012	13	278221	4694885
Green Mtn	GM 6001	13	282048	4686087
Green Mtn	GM 6002	13	281173	4686243
Green Mtn	GM 6003	13	279993	4687210
Green Mtn	GM 6004	13	278811	4686942
Green Mtn	GM 6005	13	286187	4688156
Green Mtn	GM 6006	13	284709	4688969
Green Mtn	GM 6007	13	284410	4688665
Green Mtn	GM 6008	13	283265	4693164
Green Mtn	GM 6009	13	284176	4692998
Green Mtn	GM 6010	13	284288	4693960
Horse Creek	SF 2001	12	607950	4835247
Horse Creek	SF 2002	12	607918	4834942
Horse Creek	SF 2003	12	604698	4835704
Horse Creek	SF 2004	12	607099	4835213
Horse Creek	SF 2005	12	603954	4836438
Horse Creek	SF 2006	12	609012	4836353
Horse Creek	SF 2007	12	608617	4836905

Appendix 1.1 continued.

		UTM Coordinates		
Study Area	**Plot #**	**Zone**	**Easting (m)**	**Northing (m)**
Horse Creek	SF 2008	12	613835	4841727
Horse Creek	SF 2009	12	613937	4841023
Horse Creek	SF 2010	12	608925	4835328
Horse Creek	SF 3001	12	610363	4834830
Horse Creek	SF 3002	12	610194	4835655
Horse Creek	SF 3003	12	611109	4835118
Horse Creek	SF 3004	12	612456	4835268
Horse Creek	SF 3005	12	613551	4835289
Horse Creek	SF 3006	12	613934	4835090
Horse Creek	SF 3007	12	613153	4835880
Horse Creek	SF 3008	12	612539	4836868
Horse Creek	SF 3009	12	611722	4838307
Horse Creek	SF 3010	12	610793	4837885
Laramie Peak East	LPE 5001	13	446265	4693878
Laramie Peak East	LPE 5002	13	445214	4693762
Laramie Peak East	LPE 5003	13	445858	4693099
Laramie Peak East	LPE 5004	13	445948	4692549
Laramie Peak East	LPE 5005	13	445329	4691250
Laramie Peak East	LPE 5006	13	445086	4691265
Laramie Peak East	LPE 5007	13	444774	4690872
Laramie Peak East	LPE 5008	13	441499	4692454
Laramie Peak East	LPE 5009	13	439659	4691519
Laramie Peak East	LPE 5010	13	440241	4692145
Laramie Peak East	LPE 5011	13	440740	4692504
Laramie Peak East	LPE 5012	13	447978	4688873
Laramie Peak East	LPE 5013	13	448221	4688784
Laramie Peak East	LPE 5014	13	448489	4688750
Laramie Peak East	LPE 5015	13	447784	4689470
Laramie Peak East	LPE 5016	13	448488	4689779
Laramie Peak East	LPE 6001	13	456611	4675573
Laramie Peak East	LPE 6002	13	457086	4676956
Laramie Peak East	LPE 6003	13	448392	4675159
Laramie Peak East	LPE 6004	13	450274	4676922
Laramie Peak East	LPE 6005	13	456364	4680337
Laramie Peak East	LPE 6006	13	456712	4682554
Laramie Peak East	LPE 6007	13	446010	4673269

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Laramie Peak East	LPE 6008	13	450548	4688612
Laramie Peak East	LPE 6009	13	450696	4688393
Laramie Peak East	LPE 6010	13	449823	4688301
Laramie Peak East	LPE 6011	13	449649	4688302
Laramie Peak East	LPE 9001	13	449685	4689789
Laramie Peak East	LPE 9002	13	449710	4690133
Laramie Peak West	LPW 7001	13	431851	4706414
Laramie Peak West	LPW 7002	13	431647	4706253
Laramie Peak West	LPW 7003	13	431924	4706291
Laramie Peak West	LPW 7004	13	430253	4706289
Laramie Peak West	LPW 7005	13	430406	4706221
Laramie Peak West	LPW 7006	13	431326	4700918
Laramie Peak West	LPW 7007	13	432020	4702495
Laramie Peak West	LPW 7008	13	432134	4699123
Laramie Peak West	LPW 7009	13	431797	4699696
Laramie Peak West	LPW 7010	13	432667	4703735
Laramie Peak West	LPW 7011	13	429130	4702977
Laramie Peak West	LPW 7012	13	429587	4703086
Laramie Peak West	LPW 7013	13	429735	4703071
Laramie Peak West	LPW 8001	13	419457	4706110
Laramie Peak West	LPW 8002	13	419026	4706085
Laramie Peak West	LPW 8003	13	419780	4706479
Laramie Peak West	LPW 8004	13	420103	4706398
Laramie Peak West	LPW 8005	13	418352	4708765
Laramie Peak West	LPW 8006	13	418840	4709036
Laramie Peak West	LPW 8007	13	419032	4708733
Laramie Peak West	LPW 8008	13	418670	4708443
Laramie Peak West	LPW 8009	13	417277	4706661
Laramie Peak West	LPW 8010	13	421718	4699841
Laramie Peak West	LPW 8011	13	421825	4699693
Laramie Peak West	LPW 8012	13	421910	4700071
Laramie Peak West	LPW 8013	13	422476	4700746
Laramie Peak West	LPW 8014	13	421554	4699583
Laramie Peak West	LPW 8015	13	422222	4699104
Laramie Peak West	LPW 8016	13	431659	4703021
Laramie Peak West	LPW 8017	13	432256	4702938

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Muddy Mtn	MU 4001	13	378960	4732086
Muddy Mtn	MU 4002	13	392646	4727402
Muddy Mtn	MU 4003	13	388781	4730623
Muddy Mtn	MU 4004	13	389196	4730873
Muddy Mtn	MU 4005	13	392736	4732177
Muddy Mtn	MU 4006	13	387426	4732492
Muddy Mtn	MU 4007	13	387450	4733562
Muddy Mtn	MU 4008	13	381583	4734497
Muddy Mtn	MU 4009	13	382524	4734405
Muddy Mtn	MU 5001	13	395925	4726115
Muddy Mtn	MU 5002	13	393996	4727591
Muddy Mtn	MU 5003	13	391754	4724639
Muddy Mtn	MU 5004	13	395609	4709851
Muddy Mtn	MU 5005	13	392723	4722872
Muddy Mtn	MU 5006	13	392161	4724683
Muddy Mtn	MU 5007	13	395263	4725134
Muddy Mtn	MU 5008	13	405040	4723581
Muddy Mtn	MU 5009	13	385607	4734075
Muddy Mtn	MU 5010	13	384443	4734250
Muddy Mtn	MU 5011	13	383117	4734436
Northern Snowy Range	SN 1001	13	402201	4572207
Northern Snowy Range	SN 1801	13	364590	4592831
Northern Snowy Range	SN 1802	13	364657	4592713
Northern Snowy Range	SN 1803	13	364255	4592226
Northern Snowy Range	SN 1804	13	364262	4592148
Northern Snowy Range	SN 1805	13	364618	4592175
Northern Snowy Range	SN 1806	13	364507	4594676
Northern Snowy Range	SN 1807	13	364977	4594487
Northern Snowy Range	SN 1808	13	364306	4594027
Northern Snowy Range	SN 1809	13	367461	4591287
Northern Snowy Range	SN 2001	13	393202	4603949
Northern Snowy Range	SN 2002	13	393206	4603516
Northern Snowy Range	SN 2003	13	401472	4571507
Northern Snowy Range	SN 2004	13	401837	4571576
Northern Snowy Range	SN 2005	13	391154	4601847
Northern Snowy Range	SN 2006	13	392285	4602156

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Northern Snowy Range	SN 2007	13	395229	4603608
Northern Snowy Range	SN 2008	13	395514	4603594
Northern Snowy Range	SN 2009	13	402217	4570585
Northern Snowy Range	SN 2010	13	402279	4569499
Northern Snowy Range	SN 2011	13	402175	4569451
Northern Snowy Range	SN 2012	13	402093	4568903
Northern Snowy Range	SN 2013	13	402122	4569813
Northern Snowy Range	SN 2014	13	401921	4569890
Northern Snowy Range	SN 3001	13	400448	4576719
Northern Snowy Range	SN 3002	13	400339	4576918
Northern Snowy Range	SN 3003	13	401684	4576770
Northern Snowy Range	SN 3004	13	403966	4577640
Northern Snowy Range	SN 3005	13	404039	4577475
Northern Snowy Range	SN 3006	13	406123	4591908
Northern Snowy Range	SN 3007	13	405897	4592123
Northern Snowy Range	SN 3008	13	404525	4591301
Northern Snowy Range	SN 3009	13	404117	4591554
Northern Snowy Range	SN 3010	13	404422	4591479
Northern Snowy Range	SN 3011	13	401604	4571871
Northern Snowy Range	SN 3012	13	401930	4572201
Northern Snowy Range	SN 3013	13	402157	4571585
Northern Snowy Range	SN 3014	13	401421	4573136
Northern Snowy Range	SN 3015	13	401443	4573321
Northern Snowy Range	SN 5001	13	400111	4582214
Northern Snowy Range	SN 5002	13	400185	4582313
Northern Snowy Range	SN 5003	13	400705	4582763
Northern Snowy Range	SN 5004	13	402080	4583313
Northern Snowy Range	SN 5005	13	401927	4583517
Northern Snowy Range	SN 5006	13	369781	4593332
Northern Snowy Range	SN 5007	13	368678	4593863
Northern Snowy Range	SN 5008	13	368160	4593787
Northern Snowy Range	SN 6001	13	396423	4604494
Northern Snowy Range	SN 6002	13	395397	4603916
Northern Snowy Range	SN 6003	13	394926	4605549
Northern Snowy Range	SN 6004	13	392936	4603078
Northern Snowy Range	SN 6005	13	395124	4602853

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Northern Snowy Range	SN 6006	13	398072	4601750
Northern Snowy Range	SN 6007	13	398561	4603357
Northern Snowy Range	SN 6008	13	364718	4593081
Northern Snowy Range	SN 6009	13	364670	4593033
Northern Snowy Range	SN 9006	13	403411	4575390
Northern Snowy Range	SN 9007	13	402629	4575166
Northern Snowy Range	SN 9008	13	398065	4578562
Northern Snowy Range	SN 9009	13	400295	4576191
Pole Mtn	PM 1001	13	464089	4564960
Pole Mtn	PM 1002	13	463015	4568519
Pole Mtn	PM 1003	13	473954	4572479
Pole Mtn	PM 1004	13	474547	4569770
Pole Mtn	PM 1005	13	475071	4570010
Pole Mtn	PM 1006	13	471339	4569948
Pole Mtn	PM 2001	13	471103	4557732
Pole Mtn	PM 2002	13	471068	4557863
Pole Mtn	PM 2003	13	473049	4559407
Pole Mtn	PM 2004	13	473392	4556600
Pole Mtn	PM 2005	13	473487	4556073
Pole Mtn	PM 2006	13	473693	4556613
Pole Mtn	PM 2007	13	469165	4555934
Pole Mtn	PM 2008	13	469353	4556381
Pole Mtn	PM 3001	13	471632	4558103
Pole Mtn	PM 3002	13	471745	4558094
Pole Mtn	PM 3003	13	474219	4558060
Pole Mtn	PM 3004	13	474110	4557571
Pole Mtn	PM 3005	13	468700	4558140
Pole Mtn	PM 3006	13	469141	4557743
Pole Mtn	PM 3007	13	468653	4557588
Pole Mtn	PM 3008	13	475526	4557139
Pole Mtn	PM 4001	13	461398	4567623
Pole Mtn	PM 4002	13	461441	4567679
Pole Mtn	PM 5001	13	466364	4562905
Pole Mtn	PM 5002	13	466245	4562968
Pole Mtn	PM 5003	13	467222	4561645
Pole Mtn	PM 5004	13	466947	4561736

Appendix 1.1 continued.

		UTM Coordinates		
Study Area	**Plot #**	**Zone**	**Easting (m)**	**Northing (m)**
Pole Mtn	PM 5005	13	470249	4562156
Pole Mtn	PM 5006	13	469667	4562406
Pole Mtn	PM 5007	13	468444	4560073
Pole Mtn	PM 5008	13	468823	4560168
Pole Mtn	PM 5009	13	466715	4559820
Pole Mtn	PM 5010	13	466343	4558984
Pole Mtn	PM 5011	13	470730	4559457
Pole Mtn	PM 5012	13	470762	4559733
Pole Mtn	PM 5013	13	471031	4560179
Pole Mtn	PM 5014	13	473678	4562312
Pole Mtn	PM 5015	13	472710	4562875
Pole Mtn	PM 5016	13	465727	4560801
Pole Mtn	PM 5017	13	465253	4560958
Pole Mtn	PM 5018	13	473719	4558510
Pole Mtn	PM 5019	13	464684	4561737
Pole Mtn	PM 5020	13	463816	4563581
Pole Mtn	PM 6001	13	465426	4563902
Pole Mtn	PM 6002	13	465269	4564180
Pole Mtn	PM 6003	13	465823	4564061
Pole Mtn	PM 6004	13	465645	4563555
Pole Mtn	PM 6005	13	464173	4564856
Pole Mtn	PM 6006	13	464352	4565109
Pole Mtn	PM 6007	13	462221	4564736
Pole Mtn	PM 6008	13	460724	4564866
Pole Mtn	PM 6009	13	461748	4564719
Pole Mtn	PM 6010	13	462692	4564789
Pole Mtn	PM 6011	13	465515	4567039
Pole Mtn	PM 6012	13	465578	4566580
Pole Mtn	PM 6013	13	462731	4570958
Pole Mtn	PM 6014	13	462506	4570981
Pole Mtn	PM 6015	13	463767	4567819
Pole Mtn	PM 6016	13	463807	4568949
Pole Mtn	PM 6017	13	464491	4571665
Pole Mtn	PM 6018	13	463561	4571553
Pole Mtn	PM 6019	13	464590	4569789
Pole Mtn	PM 6020	13	466318	4569852

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Pole Mtn	PM 7001	13	468446	4567553
Pole Mtn	PM 7002	13	467863	4567339
Pole Mtn	PM 7003	13	471336	4567385
Pole Mtn	PM 7004	13	474231	4567636
Pole Mtn	PM 7005	13	472320	4566384
Pole Mtn	PM 7006	13	467262	4566228
Pole Mtn	PM 7007	13	467007	4565301
Pole Mtn	PM 7008	13	472752	4564866
Pole Mtn	PM 7009	13	474536	4563370
Pole Mtn	PM 7010	13	475543	4567452
Pole Mtn	PM 8001	13	467067	4571975
Pole Mtn	PM 8002	13	467047	4571382
Pole Mtn	PM 8003	13	470767	4572168
Pole Mtn	PM 8004	13	469845	4572664
Pole Mtn	PM 8005	13	468575	4570638
Pole Mtn	PM 8006	13	468120	4570070
Pole Mtn	PM 8007	13	472908	4568374
Pole Mtn	PM 8008	13	472804	4567870
Pole Mtn	PM 8009	13	469807	4568910
Pole Mtn	PM 8010	13	467202	4568242
Pole Mtn	PM 8011	13	466371	4569073
Pole Mtn	PM 8012	13	463474	4569794
Pole Mtn	PM 8013	13	461542	4569341
Pole Mtn	PM 8014	13	461512	4569391
Pole Mtn	PM 9001	13	467849	4566761
Pole Mtn	PM 9002	13	467830	4564330
Pole Mtn	PM 9003	13	467871	4564155
Pole Mtn	PM 9004	13	472057	4564268
Pole Mtn	PM 9005	13	470274	4565392
Roosevelt N.F.	RO 2001	13	445890	4535488
Roosevelt N.F.	RO 2002	13	445282	4534832
Roosevelt N.F.	RO 2003	13	441873	4534054
Roosevelt N.F.	RO 2004	13	447117	4538555
Roosevelt N.F.	RO 2005	13	445997	4537522
Roosevelt N.F.	RO 2006	13	443998	4537472
Roosevelt N.F.	RO 2007	13	445993	4536848
Roosevelt N.F.	RO 2008	13	452238	4523797

Appendix 1.1 continued.

		UTM Coordinates		
Study Area	**Plot #**	**Zone**	**Easting (m)**	**Northing (m)**
Roosevelt N.F.	RO 2009	13	452041	4522887
Roosevelt N.F.	RO 3001	13	451020	4533451
Roosevelt N.F.	RO 3002	13	452052	4535189
Roosevelt N.F.	RO 3003	13	449101	4535859
Roosevelt N.F.	RO 3004	13	448069	4538018
Roosevelt N.F.	RO 3005	13	448653	4538110
Roosevelt N.F.	RO 3006	13	449342	4537082
Roosevelt N.F.	RO 3007	13	450251	4534466
Roosevelt N.F.	RO 3008	13	448469	4535990
Roosevelt N.F.	RO 3009	13	447927	4533157
Roosevelt N.F.	RO 3010	13	451859	4522291
Roosevelt N.F.	RO 3011	13	452464	4522095
Roosevelt N.F.	RO 4001	13	444110	4532488
Roosevelt N.F.	RO 4002	13	442117	4518452
Roosevelt N.F.	RO 4003	13	440664	4516449
Roosevelt N.F.	RO 4004	13	443785	4517569
Roosevelt N.F.	RO 4005	13	445142	4516550
Roosevelt N.F.	RO 4006	13	446451	4510712
Roosevelt N.F.	RO 4007	13	446918	4517206
Roosevelt N.F.	RO 4008	13	446955	4519067
Roosevelt N.F.	RO 5001	13	449276	4522400
Roosevelt N.F.	RO 5002	13	453276	4514490
Roosevelt N.F.	RO 5003	13	445802	4516845
Roosevelt N.F.	RO 5004	13	449359	4510452
Roosevelt N.F.	RO 5005	13	447338	4510825
Roosevelt N.F.	RO 5006	13	448125	4512129
Roosevelt N.F.	RO 5007	13	448713	4514557
Roosevelt N.F.	RO 5008	13	453668	4515588
Roosevelt N.F.	RO 5009	13	454783	4516511
Roosevelt N.F.	RO 5010	13	453763	4516999
Roosevelt N.F.	RO 5011	13	448743	4509412
Roosevelt N.F.	RO 5012	13	449393	4502611
Roosevelt N.F.	RO 5013	13	444622	4500325
Roosevelt N.F.	RO 5014	13	447198	4500675
Roosevelt N.F.	RO 6001	13	402450	4538678
Roosevelt N.F.	RO 6002	13	406406	4538633
Roosevelt N.F.	RO 6003	13	403649	4536842

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Roosevelt N.F.	RO 6004	13	404465	4532310
Roosevelt N.F.	RO 6005	13	403244	4538724
Roosevelt N.F.	RO 6006	13	403810	4538154
Roosevelt N.F.	RO 6007	13	407896	4537381
Roosevelt N.F.	RO 6008	13	408242	4530638
Roosevelt N.F.	RO 6009	13	406777	4532723
Roosevelt N.F.	RO 6010	13	406421	4533158
Roosevelt N.F.	RO 6011	13	409208	4534354
Roosevelt N.F.	RO 6012	13	408909	4533761
Roosevelt N.F.	RO 7001	13	427846	4495950
Roosevelt N.F.	RO 7002	13	426612	4523265
Roosevelt N.F.	RO 7003	13	427128	4520847
Roosevelt N.F.	RO 7004	13	428916	4526968
Roosevelt N.F.	RO 7005	13	430287	4528081
Roosevelt N.F.	RO 7006	13	431751	4527811
Roosevelt N.F.	RO 7007	13	434169	4528822
Roosevelt N.F.	RO 7008	13	433859	4528155
Roosevelt N.F.	RO 7009	13	440299	4533858
Roosevelt N.F.	RO 8001	13	456711	4537509
Roosevelt N.F.	RO 8002	13	429165	4526423
Roosevelt N.F.	RO 8003	13	422109	4531568
Roosevelt N.F.	RO 8004	13	421933	4533079
Roosevelt N.F.	RO 8005	13	425401	4534329
Roosevelt N.F.	RO 8006	13	423697	4534048
Roosevelt N.F.	RO 8007	13	401309	4538928
Roosevelt N.F.	RO 9001	13	443611	4533157
Roosevelt N.F.	RO 9002	13	444572	4532632
Roosevelt N.F.	RO 9003	13	447268	4530812
Roosevelt N.F.	RO 9004	13	445255	4531952
Roosevelt N.F.	RO 9005	13	449093	4530044
Shirley Mtn	SH 2001	13	357031	4672291
Shirley Mtn	SH 2002	13	357328	4672208
Shirley Mtn	SH 2003	13	358200	4671908
Shirley Mtn	SH 2004	13	357867	4672722
Shirley Mtn	SH 2005	13	360670	4671054
Shirley Mtn	SH 2006	13	358187	4669124
Shirley Mtn	SH 2007	13	358710	4669256

Appendix 1.1 continued.

		UTM Coordinates		
Study Area	**Plot #**	**Zone**	**Easting (m)**	**Northing (m)**
Shirley Mtn	SH 2008	13	359276	4669829
Shirley Mtn	SH 2009	13	359880	4670583
Shirley Mtn	SH 2010	13	362493	4669402
Shirley Mtn	SH 2011	13	362265	4668783
Shirley Mtn	SH 2012	13	360816	4666416
Shirley Mtn	SH 2013	13	360405	4665897
Shirley Mtn	SH 2014	13	367074	4676410
Shirley Mtn	SH 2015	13	367075	4675215
Shirley Mtn	SH 3001	13	377669	4667125
Shirley Mtn	SH 3002	13	377738	4666986
Shirley Mtn	SH 3003	13	377835	4666625
Shirley Mtn	SH 3004	13	373220	4666084
Shirley Mtn	SH 3005	13	374473	4666916
Shirley Mtn	SH 3006	13	369439	4673385
Shirley Mtn	SH 3007	13	370557	4673676
Shirley Mtn	SH 3008	13	370877	4673127
Shirley Mtn	SH 3009	13	369248	4672350
Shirley Mtn	SH 3010	13	367854	4667753
Shirley Mtn	SH 3011	13	369406	4667741
Shirley Mtn	SH 3012	13	369181	4667821
Shirley Mtn	SH 3013	13	385050	4667673
Shirley Mtn	SH 3014	13	385268	4667352
Shirley Mtn	SH 3015	13	384986	4668040
Shirley Mtn	SH 3016	13	384665	4669023
Shirley Mtn	SH 3017	13	369016	4673484
Shirley Mtn	SH 3018	13	367859	4674119
Sierra Madre	SM 1801	13	372878	4542211
Sierra Madre	SM 1802	13	370571	4543072
Sierra Madre	SM 1803	13	373050	4541291
Sierra Madre	SM 2001	13	368467	4541070
Sierra Madre	SM 2002	13	368448	4541480
Sierra Madre	SM 2003	13	365638	4542738
Sierra Madre	SM 2004	13	368621	4540637
Sierra Madre	SM 2005	13	324984	4571303
Sierra Madre	SM 2006	13	322837	4575019
Sierra Madre	SM 2007	13	324425	4574732
Sierra Madre	SM 2008	13	324342	4573752

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Sierra Madre	SM 2009	13	331520	4573579
Sierra Madre	SM 2010	13	331132	4574171
Sierra Madre	SM 2011	13	331280	4574437
Sierra Madre	SM 2012	13	333307	4571974
Sierra Madre	SM 2013	13	332394	4572228
Sierra Madre	SM 2014	13	332322	4571815
Sierra Madre	SM 2015	13	331296	4571752
Sierra Madre	SM 3001	13	353179	4554688
Sierra Madre	SM 3002	13	353674	4553955
Sierra Madre	SM 3003	13	354884	4551725
Sierra Madre	SM 3004	13	361074	4549647
Sierra Madre	SM 3005	13	360295	4550594
Sierra Madre	SM 3006	13	359933	4550825
Sierra Madre	SM 3007	13	362416	4550734
Sierra Madre	SM 3008	13	354077	4553611
Sierra Madre	SM 3009	13	361493	4549381
Sierra Madre	SM 3010	13	361555	4550507
Sierra Madre	SM 3011	13	362538	4551262
Sierra Madre	SM 3012	13	339521	4559519
Sierra Madre	SM 3013	13	335893	4566644
Southern Snowy Range	SS 1801	13	411669	4569495
Southern Snowy Range	SS 1802	13	412948	4554848
Southern Snowy Range	SS 1803	13	413254	4557160
Southern Snowy Range	SS 1804	13	412829	4557623
Southern Snowy Range	SS 1805	13	413333	4558893
Southern Snowy Range	SS 1806	13	414520	4560938
Southern Snowy Range	SS 1807	13	415429	4561816
Southern Snowy Range	SS 1808	13	412538	4558449
Southern Snowy Range	SS 1809	13	410608	4558180
Southern Snowy Range	SS 5001	13	410409	4552880
Southern Snowy Range	SS 5002	13	409443	4546380
Southern Snowy Range	SS 5003	13	410379	4546479
Southern Snowy Range	SS 5004	13	410421	4546117
Southern Snowy Range	SS 5005	13	410020	4546053
Southern Snowy Range	SS 6001	13	384674	4541430
Southern Snowy Range	SS 6002	13	384576	4541195
Southern Snowy Range	SS 6003	13	383109	4540955

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Southern Snowy Range	SS 6004	13	382311	4546263
Southern Snowy Range	SS 7001	13	402219	4560254
Southern Snowy Range	SS 7002	13	402025	4560244
Southern Snowy Range	SS 7003	13	400795	4561453
Southern Snowy Range	SS 7004	13	402169	4562009
Southern Snowy Range	SS 7005	13	402954	4561367
Southern Snowy Range	SS 7006	13	402236	4560827
Southern Snowy Range	SS 7007	13	404094	4560561
Southern Snowy Range	SS 7008	13	401052	4563968
Southern Snowy Range	SS 7009	13	401195	4564272
Southern Snowy Range	SS 7010	13	401071	4564467
Southern Snowy Range	SS 7011	13	400679	4564672
Southern Snowy Range	SS 7012	13	400886	4564744
Southern Snowy Range	SS 7013	13	400749	4564316
Southern Snowy Range	SS 7014	13	401095	4563525
Southern Snowy Range	SS 7015	13	402130	4563315
Southern Snowy Range	SS 7016	13	402497	4563497
Southern Snowy Range	SS 7017	13	402317	4564629
Southern Snowy Range	SS 7018	13	402437	4564250
Southern Snowy Range	SS 7019	13	413177	4553444
Southern Snowy Range	SS 7020	13	413192	4553273
Southern Snowy Range	SS 7021	13	412104	4552798
Southern Snowy Range	SS 7022	13	411039	4552916
Southern Snowy Range	SS 7023	13	412086	4553305
Southern Snowy Range	SS 7024	13	382874	4543058
Southern Snowy Range	SS 8001	13	408315	4550642
Southern Snowy Range	SS 8002	13	407281	4550437
Southern Snowy Range	SS 8003	13	408802	4551783
Southern Snowy Range	SS 8004	13	408339	4550212
Southern Snowy Range	SS 8005	13	409105	4550737
Southern Snowy Range	SS 8006	13	409205	4550275
Southern Snowy Range	SS 8007	13	409624	4551319
Southern Snowy Range	SS 8008	13	411562	4542722
Southern Snowy Range	SS 8009	13	409251	4542417
Southern Snowy Range	SS 8010	13	408728	4542854
Southern Snowy Range	SS 8011	13	410817	4543052
Southern Snowy Range	SS 8012	13	410407	4542945

Appendix 1.1 continued.

Study Area	Plot #	UTM Coordinates Zone	Easting (m)	Northing (m)
Southern Snowy Range	SS 8013	13	409040	4543252
Southern Snowy Range	SS 8014	13	406790	4539855
Southern Snowy Range	SS 8015	13	406914	4540181
Southern Snowy Range	SS 8016	13	407720	4539385
Southern Snowy Range	SS 8017	13	409176	4540700
Southern Snowy Range	SS 8018	13	409674	4540947
Southern Snowy Range	SS 8019	13	417948	4550056
Southern Snowy Range	SS 8020	13	418061	4550262
Southern Snowy Range	SS 8021	13	416802	4548584
Southern Snowy Range	SS 8022	13	416450	4547488
Southern Snowy Range	SS 8023	13	417375	4547226
Southern Snowy Range	SS 8024	13	416507	4546027
Southern Snowy Range	SS 8025	13	409584	4539233
Southern Snowy Range	SS 8026	13	409737	4539080
Southern Snowy Range	SS 8027	13	411719	4546534
Wind River Ind. Res.	WR 1001	12	652758	4762109
Wind River Ind. Res.	WR 1002	12	652616	4762597
Wind River Ind. Res.	WR 1003	12	653488	4761404
Wind River Ind. Res.	WR 1004	12	654865	4763141
Wind River Ind. Res.	WR 1005	12	659072	4752605
Wind River Ind. Res.	WR 1006	12	660494	4754940
Wind River Ind. Res.	WR 1007	12	660986	4755078
Wind River Ind. Res.	WR 1008	12	660389	4752948
Wind River Ind. Res.	WR 1009	12	660634	4752926
Wind River Ind. Res.	WR 1010	12	661735	4753655
Wind River Ind. Res.	WR 2001	12	652746	4759672
Wind River Ind. Res.	WR 2002	12	653605	4760056
Wind River Ind. Res.	WR 2004	12	660255	4751806
Wind River Ind. Res.	WR 2005	12	661270	4749655
Wind River Ind. Res.	WR 2006	12	660967	4749884

Chapter 2.

The distribution and density of *Ribes*, the alternate host of *Cronartium ribicola*, in Colorado and Wyoming

Introduction

Species in the genus *Ribes*, commonly known as gooseberries and currants, act as the alternate host for the exotic, invasive forest pathogen *Cronartium ribicola* (J. C. Fischer ex Rabh.), the causal agent of white pine blister rust. In order for the pathogen to complete its lifecycle and infect 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)), three spore stages are produced on the *Ribes* host. In western North America, the impact of *C. ribicola* on the *Ribes* host is minimal, typically causing only late season defoliation under severe infestations (Mielke 1943). *Ribes* are typically infected by aeciospores produced on white pines in the spring. Following germination of the aeciospores, germ tubes of aeciospores enter the *Ribes* host through stomata (Mielke 1943). Following an incubation period of two to three weeks, uredinia are produced usually on the lower side of the *Ribes* leaf, but they may also develop on leaf petioles, green fruits, floral bracts, cotyledons, bud scales, peduncles, and young stems (Mielke 1943, Spaulding 1922). Urediniospores, produced in the uredinia, serve to intensify the rust on the *Ribes* host by reinfecting the host and adjacent *Ribes* bushes. As a general rule, the more generations of uredinia that occur within the growing

season, the greater the number of telia that may be formed and, thus, the higher the production of inocula for pine infection (Mielke 1943). In the Pacific Northwest and British Columbia, though two to seven generations may occur, generally four or five generations of uredinia develop. The number of generations produced depends on the amount of moisture, which is necessary for the germination of the urediniospores, the *Ribes* species, and locality (Mielke 1943). The earliest telia produced in the season develop from old uredinia. Telia may be produced throughout the growing season, but their production appears to be stimulated by the onset of cooler autumn temperatures (Mielke 1943). The pine-infecting spores, or basidiospores, are formed on the telia; the amount of telia produced is indicative of the amount of pine-infecting inocula that will be produced.

Species of *Ribes* vary dramatically in their susceptibly to *C. ribicola* and productivity in terms of the amount of pine-infecting basidiospores that are produced. Several species of *Ribes* are known to occur in Colorado and Wyoming over a wide variety of habitats including: *Ribes americanum* Mill., *R. aureum* Pursh, *R. cereum* Dougl., *R. hudsonianum* Richards., *R. inerme* Rydb., *R. lacustre* (Pers.) Poir., *R. laxiflorum* Pursh, *R. leptanthum* A. Gray, *R. montigenum* McClat., *R. oxycanthoides* L. var. *oxycanthoides*, *R. oxycanthoides* L. var. *setosum* (Lindl.) Dom., *R. viscosissimum* Pursh, *R. wolfii* Rothrock, (Van Arsdel and Geils 2004, Hartman and Nelson 2001, Nelson and Hartman 1994). For the purposes of this paper the naming conventions of Van Arsdel and Geils (2004) are employed.

White pine blister rust (WPBR) was first reported in northern Colorado in 1998 on the Roosevelt National Forest (Johnson and Jacobi 2000). A survey was conducted and found that all infected limber pines (*Pinus flexilis* James) were located within approximately 18 km of the Wyoming border (Johnson and Jacobi 2000). There exists the possibility that WPBR will spread naturally or be introduced throughout the range of white pines in Colorado and southeastern Wyoming, which includes scattered populations of limber, southwestern white (*P. strobiformis* Engelm.), and Rocky Mountain bristlecone pines (*P. aristata* Engelm.). It was not known at the time of this study which, if any, species of *Ribes* grow within and in the vicinity of native white pine stands. Because species of *Ribes* differ in their potentials for production of pine-infecting basidiospores, it is important when examining the epidemiology of this disease to gain knowledge of the distribution and density of individual species of *Ribes*. We hypothesized that some species of *Ribes* would be present throughout the range of white pines in Wyoming and Colorado, but that the species and density would vary by site conditions. Knowledge of the distribution of *Ribes* and their associated site conditions may, in turn, aid in predicting where damage to white pines from white pine blister rust may be most likely to occur. The objectives of this survey were to 1) determine the distribution of *Ribes* species growing within and in the vicinity of native white pine stands in Colorado and Wyoming, and 2) determine if any site variables can predict *Ribes* occurrence and density.

Methods

Study areas

Surveys occurred on 15 study areas in Colorado and Wyoming. Study areas in Colorado (Figure 2.1) were defined by National Forest (N.F.) boundaries and included the Arapahoe, Pike, Rio Grande, Roosevelt, and San Isabel N.F.s. Wyoming study areas (Figure 2.2) were defined by government management units and geographic locations and included the Horse Creek area of the Shoshone N.F.; Wind River Indian Reservation, on lands managed by the Bureau of Indian Affairs (BIA); Green Mountain, Shirley Mountains, and Muddy Mountain, on lands managed by the Bureau of Land Management (BLM); and the Laramie Peak, Sierra Madre, Snowy Range (divided into northern and southern study areas for the purposes of this study), and Pole Mountain areas of the Medicine Bow N.F..

Plot selection

Two surveys, an intensive pine/*Ribes* survey and an extensive *Ribes* survey, were conducted to determine *Ribes* occurrence and density on 11 of the study areas. On the remaining four study areas (the Arapahoe, Pike, Rio Grande, and San Isabel N.F.s) only the extensive survey was conducted, as these areas were not surveyed for white pine blister rust. The pine/*Ribes* survey was conducted to assess *Ribes* occurrence and density within limber pine stands surveyed for white pine blister rust (Kearns 2005, Chapter 1).

Pine/Ribes Survey

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 (RMRIS) database. Digital Ortho Quadrangles were obtained from the Roosevelt and Medicine Bow National Forests and maps created to direct the sampling effort in these areas. Post-stratification 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, on all aspects, topographic positions, and forest composition types available for sampling. Surveyed stands were within three kilometers of a road to limit travel time between stands and maximize the number of plots established. Paper maps were obtained for areas managed by Bureau of Land Management and Bureau of Indian Affairs. Surveys in non-Forest Service managed areas were directed to locations recommended by employees familiar with the areas as having significant populations of limber pine.

Extensive Survey

Extensive survey plots also were within three kilometers of a road. In study areas that were also surveyed for white pine blister rust, attempts were made to locate extensive survey plots within one kilometer of white pine plots. In Colorado, study areas not surveyed for WPBR (the Arapahoe, Pike, Rio Grande, and San Isabel N.F.s), extensive survey plots were located to represent the breadth of *Ribes* habitats within 2 km of stands of limber and Rocky Mountain (RM) bristlecone pines.

Survey methods

Pine/Ribes Survey

Belt transects (30.5 by 4.6 m) were established at the end of white pine health survey transects (Kearns 2005, Chapter 1) in 504 pine/*Ribes* survey plots to examine the *Ribes* growing amidst limber pines. Two or three *Ribes* transects defined the plot. The *Ribes* species present, total number of stems or bushes, average number of stems per bush, and average stem length were recorded. The variability in the number of stems per bush required a count of stems present rather than number of bushes alone. The series of *Ribes* transects at each plot were summed and from these data densities of *Ribes* by species in linear meters of live stem per hectare (m/ha) were calculated. At each plot, elevation, percent slope, slope aspect, slope position, slope configuration, stand structure were recorded. In addition, to gain a perspective of the vegetative composition of the site, the three most common overstory trees species and the three most dominant understory cover types, a combination of species and broad cover type classifications such as rock or litter, were also recorded. Using these methods 504 pine/*Ribes* plots were established from mid-May through September of 2002, 2003, and 2004.

Extensive Survey

In addition to surveying the *Ribes* growing among native white pine populations, we performed an extensive survey to examine *Ribes* populations growing within 2 km of native white pines. Plots were located as described above and sampled by a 61 by 6.1 m belt transect. We used a larger belt transect to survey extensive *Ribes* because only one transect defined the plot. The GPS coordinates of the starting point of the transect were recorded. The identical data were collected as described in the pine/*Ribes* survey. In

addition, a description of the site (riparian, meadow, forested/wooded, wetland) was recorded to gain a perspective of the general site conditions. During mid-May through September of 2002, 2003, and 2004, 754 extensive survey plots were established in Wyoming and Colorado.

Data analyses

All statistical analyses were performed utilizing SAS (version 9.1) statistical program. Tukey's honest significant difference (HSD) was used for multiple comparisons of means because it is recommended for unequal sample sizes and is considered conservative in that it has a low type I error rate (falsely rejecting the null hypothesis) and shows fewer significant differences (P. Chapman, pers. comm.) such that variables are more likely to be useful in model building. To examine the differences in *Ribes* densities and for modeling purposes, *Ribes* densities were transformed to $\log_{10}$ scale, in order to reduce the extreme skewness in the data. All density means presented are in $\log_{10}$ scale (standard error (SE)) unless otherwise noted. Logistic regression, using stepwise model selection, was used to estimate the odds of finding individual *Ribes* species based on site criteria. Final model selection was based on the model that provided a maximum Kappa statistic and area under the receiver operating characteristic curve. To assess the effectiveness of a predictor variable in correctly classifying observations, measuring the improvement over chance agreement is necessary (Fielding and Bell 1997). The Kappa statistic (K) provides a measure of prediction accuracy while incorporating a correction for chance-expected agreement (Fleiss 1981, Fielding and Bell 1997). Kappa statistic values <0.4 indicate poor agreement, $0.4<K<0.75$ indicate good agreement, and $K>0.75$ indicates

excellent agreement (Fielding and Bell 1997). The area under the receiver operating characteristic (ROC) curve is another measure of overall model accuracy. Values for areas under the ROC curve (AUC) range from 0.5 to 1.0, and indicate the proportion of time that a random observation in the positive category will have a greater score than a random observation from the negative category (Fielding and Bell 1997).

Results

Distribution and density by *Ribes* species

Ribes cereum

Ribes cereum, wax currant (Figure 2.3), was the most commonly encountered *Ribes* species and was present on 33% (416 of 1258) of all established plots: on 26% (194 of 754) of the extensive survey plots and on 44% (222 of 504) pine/*Ribes* plots. *Ribes cereum* was present in all of the 15 study areas. Densities of *R. cereum* ranged from 0 to 37,401 m/ha with a mean density of 590 m/ha (SE 62) on the 1258 plots. In the $\log_{10}$ scale, densities ranged from 0 to 4.57 and averaged 0.91 (SE 0.04) over the 1258 plots. There were significant differences ($p<0.05$) in mean $\log_{10}$ *R. cereum* density among the 15 study areas (Table 2.1), with the highest mean $\log_{10}$ *R. cereum* density occurring at Pole Mountain, 1.88 (SE 0.08), and the lowest mean $\log_{10}$ density recorded at the Shoshone N.F. study site, 0.24 (SE 0.24). The proportion of plots occupied by wax current within individual study areas ranged from 68% at Pole Mountain to 11% the Shoshone N.F. study area. Plots with *R. cereum* ranged in elevation from 1884 to 3414 m. Of the 416 plots with records of wax currant, 64% (267) occurred in stands with limber pine as one of the three dominant tree species, 48% (201) with aspen (*Populus*

tremuloides Michx.), 30% (124) were in stands with ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), 30% (124) occurred with lodgepole pine (*P. contorta* var. *latifolia* Dougl. ex Loud.), 20% (85) with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and 7% (31) had a dominant component of subalpine fir (*Abies bifolia* A. Murr.). The 504 pine/*Ribes* plots had a statistically significantly greater mean $\log_{10}$ density at 1.15 based on Tukey's HSD than did the 754 extensive survey plots at 0.74, indicating that wax currant densities are higher in limber pine stands than in the other types of sites sampled. The mean $\log_{10}$ density of *R. cereum* was not significantly different in the 918 Wyoming plots (0.92 (SE 0.04) versus the 340 Colorado plots (0.86 (SE 0.07).

Ribes inerme

Ribes inerme, whitestem gooseberry (Figure 2.4), was found in all of the 15 study areas on 29% (365 of 1258) of the *Ribes* plots established. Whitestem gooseberry was recorded more commonly in the extensive survey plots with 44% (329 of 754) occupied than in the pine/*Ribes* plots with 7% (36 of 504) occupied. *Ribes inerme* densities were extremely variable, ranging from 0 to 209,973 m/ha and averaging 2027 m/ha (SE 325) across the 1258 plots. In the $\log_{10}$ scale, densities ranged from 0 to 5.32 and averaged 0.94 (SE 0.04) over the 1258 plots. Mean $\log_{10}$ density of *R. inerme* was highest in the Pole Mountain study area at 1.57 (SE 0.10) and lowest on the Arapahoe N.F. plots at 0.14 (SE 0.52) (Table 2.2), a difference in mean density $\log_{10}$ that was statistically significant at p=0.05. The proportion of plots occupied by whitestem gooseberry within individual study areas ranged from 47% at Pole Mountain to 6% at the Sierra Madre. Elevations of plots on which *R. inerme* occurred ranged from 1747 m to 3597 m (Table 2.2).

Whitestem gooseberry was found growing in association with aspen on 55% (202) of the 365 plots that had records of *R. inerme*, willow on 50% (182), limber pine on 30% (108), lodgepole pine on 25% (91), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) on 21% (76), subalpine fir on 12% (42), ponderosa pine on 11% (40), and 10% (37) of plots had Douglas-fir as one of the three dominant tree species on the site. There were significant differences ($p<0.05$) in mean density between the extensive survey plots and the pine/*Ribes* plots with the extensive survey plots having a mean $\log_{10}$ density of 1.43 compared to a mean of 0.20 on the pine/*Ribes* plots, indicating that densities are lower in limber pine stands than elsewhere on the landscape. Mean $\log_{10}$ *R. inerme* density was significantly greater in the 340 Colorado plots than in the 918 Wyoming plots, 1.08 (SE 0.08) and 0.89 (SE 0.05), respectively.

Ribes lacustre

Ribes lacustre, prickly currant (Figure 2.5), was present on 8% (99 of 1258) of established plots, 13% (95 of 754) of extensive survey plots established in 7 of the 15 study areas (Table 2.3) and 1% (4 of 504) of pine/*Ribes* plots. Overall mean density of *R. lacustre* was 266 m/ha (SE 47); densities ranged from 0 to 23,786 m/ha. In the $\log_{10}$ scale, prickly currant densities ranged from 0 to 4.38 and averaged 0.25 (SE 0.02) over the 1258 plots. Mean $\log_{10}$ density was significantly higher within the Snowy Range North study area (1.02 (SE 0.07)) than in all other study areas except the Sierra Madre (Table 2.3). The Snowy Range North study area also had the highest proportion of plots occupied by prickly currant with 30%. *Ribes lacustre* was found on plots ranging in elevation from 2321 to 3101 m. Tree species listed among the three most common on

sites with the presence of *R. lacustre* were subalpine fir on 69 (70%), Engelmann spruce on 63 (64%), lodgepole pine on 45 (45%), alder (includes *Alnus tenuifolia* Nutt. and other unidentified *Alnus* species) on 31 (31%), aspen on 30 (30%), and limber pine on 10 (10%) plots with *R. lacustre*. Mean density of *R. lacustre* varied significantly between the extensive survey plots, which had a significantly higher mean $\log_{10}$ density of 0.40 (SE 0.03), and the pines/*Ribes* plots, which had a mean $\log_{10}$ density of 0.02 (SE 0.04). Densities of *R. lacustre* were significantly greater in the Wyoming plots (0.32 (SE 0.03) compared to the Colorado plots (0.06 (SE 0.05)).

Ribes montigenum

Ribes montigenum, gooseberry currant (Figure 2.6), was present on 6% (77 of 1258) of established plots, 10% (72 of 754) of the extensive survey plots and 1% (5 of 504) pine/*Ribes* plots. Plots with records of *R. montigenum* were present in 6 of the 15 study areas (Table 2.4). Densities of *R. montigenum* ranged from 0 to 51,050 m/ha and averaged 450 m/ha (SE 94) for the 1258 plots. In the $\log_{10}$ scale, gooseberry currant densities ranged from 0 to 4.71 and averaged 0.21 (SE 0.02) over the 1258 plots. Mean $\log_{10}$ densities of alpine prickly currant were significantly higher within the Rio Grande and Pike N.F.s of Colorado (1.73 and 1.22, respectively) than in any other study areas (Table 2.4). The proportion of plot occupied was highest in the Rio Grande N.F. study area at 48%. Elevations of plots on which *R. montigenum* occurred ranged from 2670 m to 3658 m (Table 2.4). Presence of *R. montigenum* was most commonly associated with the following three most common overstory species recorded on the site: Engelmann spruce on 88% (68), subalpine fir on 36% (28), RM bristlecone pine on 17% (13),

lodgepole pine on 13% (10), and limber pine on 10% (8) of plots with records of *R. montigenum*. Mean $\log_{10}$ density was significantly higher ($p<0.05$) in the extensive survey plots at 0.33 (SE 0.03) compared to 0.03 (SE 0.04) mean density on the pine/*Ribes* plots. There were also significant differences between the states with the Colorado plots having a significantly higher mean $\log_{10}$ *R. montigenum* density, 0.69 (SE 0.04), than the Wyoming plots, 0.03 (SE 0.03).

Other *Ribes* Species

Three other species of *Ribes* were found only rarely. *Ribes laxiflorum*, trailing black currant, was present in three of the areas studied (Pike, San Isabel, and Rio Grande N.F.s), all of which are located in Colorado. *Ribes laxiflorum* was found on 5 of the 754 extensive survey plots (0.7%) with $\log_{10}$ densities that ranged from 0 to 3.66 and averaged 0.02 (SE 0.01). *Ribes laxiflorum* was not recorded in any of the 504 pines/*Ribes* plots. Elevations of plots with records of *R. laxiflorum* ranged from 2966 to 3330 m. *Ribes laxiflorum* was found growing in stands with Engelmann spruce, subalpine fir, aspen, lodgepole pine, and RM bristlecone pine listed among the three dominant tree species. *Ribes hudsonianum*, northern black currant, was present on 4 of the 754 (0.5%) extensive survey plots, all of which were located within the Wind River Indian Reservation study area in Wyoming and was not recorded in any of the 504 pine/*Ribes* plots. Mean $\log_{10}$ density of *R. hudsonianum* within the 9 extensive survey plots established on the Wind River Indian Reservation was 1.29 (SE 0.08), and over the 754 extensive survey plots *R. hudsonianum* averaged 0.02 (SE 0.01). *Ribes hudsonianum* was found on plots that ranged in elevation from 2475 to 2681 m. Dominant tree species

in plots with *R. hudsonianum* were aspen, Douglas-fir, lodgepole pine, limber pine, and alder. *Ribes viscosissimum*, sticky currant, was recorded on only 1 of the 754 (0.1%) extensive survey plots, located in the Laramie Peak study area of the Medicine Bow N.F. in Wyoming, and in none of the 504 pine/*Ribes* plots. That plot was located at 2393 m elevation and the $\log_{10}$ density of *R. viscosissimum* within that plot was 2.00 $\log_{10}$m/$\log_{10}$ha. Engelmann spruce, subalpine fir, lodgepole pine, and *R. lacustre* were growing in association with *R. viscosissimum*.

Relationships between density and site variables

Relationships between site variables and *Ribes* densities were explored for *R. cereum*, *R. inerme*, *R. lacustre*, and *R. montigenum* only, as the other species were found rarely and had too few occurrences of types of site data available.

Ribes cereum

Ribes cereum $\log_{10}$ densities were significantly, though weakly, negatively correlated with elevation ($r=-0.22$, $p<0.0001$) and positively correlated with percent slope ($r=0.19$, $p<0.0001$). Densities of *R. cereum* varied significantly by site (Figure 2.7, Appendix 2.1). The highest $\log_{10}$ densities occurred on sites described as meadows and in those plots placed in limber pine stands, while significantly lower *R. cereum* $\log_{10}$ densities were found on sites described as forested, riparian, and wetland. Plots located in valley bottoms had significantly lower $\log_{10}$ stem densities (0.64) than did plots in any other slope position categories (Figure 2.8, Appendix 2.2). Plots located in stands with closed canopies had significantly lower $\log_{10}$ stem densities (0.64) than did stands with open

canopies (1.05) or those described as a mosaic of both open and closed canopies (1.01) (Figure 2.9, Appendix 2.3). There were no significant differences in *R. cereum* $\log_{10}$ densities by slope configuration or slope aspect (Figure 2.10, Appendix 2.4). Paired t-tests determined that wax current $\log_{10}$ densities were significantly greater when ponderosa pine ($p<0.0001$) and Douglas-fir ($p=0.037$) were among the three dominant tree species on the site compared to sites without those species. *Ribes cereum* $\log_{10}$ densities were significantly lower on sites with lodgepole pine ($p<0.0001$) and subalpine fir ($p=0.001$) among the three dominant tree species compared to plots without these species. Log_{10} densities of *R. cereum* differed significantly depending on the presence or absence of various ground cover types, of which only the dominant three were recorded. Significantly greater *R. cereum* $\log_{10}$ densities were associated with plots having big sage (*Artemisia tridentata* Nutt.), common juniper (*Juniperus communis* L.), and rock while significantly lower $\log_{10}$ densities were associated with the presence of willow (various unidentified *Salix* species) and leaf litter. These data suggest that $\log_{10}$ *R. cereum* densities are higher in lower elevation, dry, open areas than in moist, densely forested areas.

Ribes inerme

Ribes inerme $\log_{10}$ densities were significantly, though weakly, negatively correlated with elevation ($r=-0.21$, $p<0.0001$) and percent slope ($r=-0.24$, $p<0.0001$). Log_{10} densities of *R. inerme* varied by site (Figure 2.7) with significantly higher $\log_{10}$ densities occurring in sites described as riparian (1.75) and wetland (1.57) than in limber pine stands (0.20), other forested (0.78), or meadow sites (0.85). Slope position (Figure 2.8) was also

associated with significant differences in $\log_{10}$ *R. inerme* densities; plots located in valley bottoms had significantly higher $\log_{10}$ densities (1.66) than did any other slope position categories. Slope configuration had no significant relationship with $\log_{10}$ *R. inerme* densities. Significantly greater $\log_{10}$ densities were found in non-forested areas (stand type equals none) than in stands characterized as having open, closed, or a mosaic of open and closed canopies (Figure 2.9). Higher $\log_{10}$ densities were associated with plots on eastern and northeastern aspects (1.32 and 1.25 $\log_{10}$m/ $\log_{10}$ha, respectively) than plots located on western, northwestern, or northern aspects (0.61, 0.61, 0.69, respectively) (Figure 2.10). Presence or absence of dominant tree species showed significant differences, based on paired t-tests, in $\log_{10}$ *R. inerme* densities. Higher $\log_{10}$ densities were found on sites with aspen as a dominant component ($p=0.0007$), and lower $\log_{10}$ *R. inerme* densities were associated with sites with lodgepole pine ($p<0.0001$), limber pine ($p<0.0001$), Engelmann spruce ($p<0.0001$), subalpine fir ($p<0.0001$), ponderosa pine ($p=0.0075$), and Douglas-fir ($p=0.0097$) as dominant components. Dominant understory cover types were also associated with significant differences in $\log_{10}$ *R. inerme* densities based on paired t-tests. Significantly higher $\log_{10}$ densities were found on sites with willows dominating the understory compared to sites without willows, and significantly lower $\log_{10}$ *R. inerme* densities were associated with sites that had common juniper, big sage, and leaf litter recorded as dominating the understory when compared to plots without those cover types dominating the understory. These data indicate that whitestem gooseberry $\log_{10}$ densities are likely to be highest on lower elevation, riparian and wetlands areas with gentle slopes and components of aspen and willow.

Ribes lacustre

There were no significant correlations between $\log_{10}$ density of *R. lacustre* and elevation or percent slope. Significantly greater $\log_{10}$ densities were found on sites described as riparian (0.63) than on any other site (Figure 2.7). Correspondingly, *R. lacustre* $\log_{10}$ densities were significantly higher in plots located in valley bottoms than in plots in other slope position categories (Figure 2.8). Plots located in stands described as having closed canopies had significantly greater $\log_{10}$ densities than did stands described as open, a mosaic of open and closed canopies or those plots which were non-forested (Figure 2.9). Plots located on northeastern aspects had significantly higher $\log_{10}$ densities of *R. lacustre* than those located on southern, southwestern, western, and northwestern aspects (Figure 2.10). Significantly greater $\log_{10}$ densities of *R. lacustre* were associated with the presence of subalpine fir, alder, and Engelmann spruce when compared by paired t-tests to plots without those species as dominant overstory cover types. Log_{10} densities were also significantly higher ($p=0.0011$) in plots with leaf litter listed as a dominant understory cover type, which likely corresponds with the significantly higher densities found in closed canopy stands. These data suggest that the highest densities of *R. lacustre* are likely to be associated with riparian areas and closed canopy forests with components of Engelmann spruce, subalpine fir, and alder.

Ribes montigenum

Log_{10} *R. montigenum* densities were fairly strongly positively correlated with elevation ($r=0.55$, $p<0.0001$). Elevation alone explained 27% of the variance in $\log_{10}$ *R.*

montigenum densities (F=443.12, p<0.0001, numerator degrees of freedom (ndf)=1, denominator degrees of freedom (ddf)=1209, R^2=0.268). Log_{10} *R. montigenum* densities were negatively correlated with GPS position (UTM northing coordinates in meters) (r=-0.43, p<0.0001), indicating that log_{10} densities were higher in more southerly located plots, i.e. Colorado locations. The UTM northing position alone explained 19% of the variance in log_{10} *R. montigenum* densities (F=275.83, p<0.0001, ndf=1, ddf=1209, R^2=0.186). No other continuous variables were significantly correlated with log_{10} *R. montigenum* densities. The highest log_{10} *R. montigenum* densities were recorded in forested sites, which had significantly greater log_{10} densities than meadow sites, or riparian, wetland, and limber pine forest sites all of which had significantly lower log_{10} densities than the first 2 sites (Figure 2.7). *R. montigenum* log_{10} densities were greatest in plots located at slope bases and significantly lower log_{10} densities were recorded on plots located in valley bottoms, slope summits/ridges, and slope shoulders (Figure 2.8). Stands described as having an open canopy had significantly greater log_{10} densities of *R. montigenum* than any other stand types (Figure 2.9). There were no significant differences in *R. montigenum* log_{10} densities by slope configuration or slope aspect class (Figure 2.10). Significantly greater log_{10} densities were associated with plots having Engelmann spruce (p<0.0001) listed as a dominant overstory component compared by paired t-test to those plots without Engelmann spruce. No comparisons between presence and absence of understory cover types were considered significant due to small sample sizes (i.e. n with *R. montigenum* and understory cover type less than 30). These data indicate that the highest log_{10} densities of gooseberry currant will be found in more southerly locations in high elevation, open stands of Engelmann spruce.

Predicting the presence of *Ribes* by species

Using the site variables discussed above, logistic regressions were run for each of the 4 *Ribes* species to predict the types of sites on which those species were likely to occur. Individual site variables were only considered for logistic regression if they exhibited significant differences in $\log_{10}$ densities for the *Ribes* species under consideration. All first order interactions between selected variables were also tested for inclusion in the models.

Ribes cereum

The logistic regression model for predicting the occurrence of *R. cereum* included 5 variables (Table 2.5). The odds of a site having *R. cereum* increased with percent slope and the presence of ponderosa pine as a dominant in the overstory. The odds of a site having *R. cereum* decreased with increasing elevation and the presence of lodgepole pine and subalpine fir as dominant overstory components. The Kappa statistic was low relative to the other species modeled at 0.324 indicating poor agreement between predicted and actual presence of *R. cereum*. Area under the ROC curve was 0.782. The model accurately predicted the presence of *R. cereum* in only 39.4% of cases and accurately predicted the absence of *R. cereum* in 89.7% of cases. Overall, the model correctly classified 73.1% of the 1245 plots used to develop the model. These data suggest that low elevation, xeric sites with overstories dominated by ponderosa pine are likely habitats for *R. cereum* in central and southeastern Wyoming and Colorado.

Ribes inerme

The selected logistic regression model for predicting the presence of *R. inerme* (Table 2.6) includes 8 variables. The odds of *R. inerme* on a site increases with the presence of an overstory composed of aspen and willow. The odds of finding *R. inerme* on a site was nearly 11 times greater in riparian areas, 9 times greater in forested areas other than limber pine stands, and nearly 8 times greater in wetland areas compared to limber pine stands. Odds of occurrence decreased with increasing elevation, with the presence of lodgepole pine and subalpine fir as dominant overstory components, and with the presence of big sage as dominant understory cover. The Kappa statistic for the selected model was 0.526, indicating fair to good agreement between actual and predicted occurrence of *R. inerme*. The AUC was 0.863. The model accurately predicted the presence of *R. inerme* in 58.1% of cases and accurately predicted the absence of *R. inerme* in 91.3% of cases. Overall, the model correctly classified 81.7% of the 1256 plots used to develop the model. The model suggests that lower elevation, mesic sites with components of aspen and willow are likely habitats for *R. inerme* in central and southeastern Wyoming and Colorado.

Ribes lacustre

The logistic regression model for predicting the probability of *R. lacustre* includes 5 variables and is presented in Table 2.7. The model indicates that probability of occurrence *R. lacustre* increases with the presence of subalpine fir, alder, and Engelmann spruce as dominant overstory components. Site also influences the odds of finding *R. lacustre* with higher odds associated with riparian (18x) and wetland sites (10x) as

compared to the odds of finding *R. lacustre* in limber pine stands and lower odds associated with meadow and other forested sites. Leaf litter as a dominant understory cover type was associated with greater odds of *R. lacustre* occurrence. In most cases, leaf litter is a dominant cover type in densely forested areas and where growing conditions are inadequate to support shrub and herbaceous cover. The Kappa statistic was 0.489 indicating only fair agreement between predicted and actual occurrence of *R. lacustre*, but the AUC was 0.917. The model accurately predicted the presence of *R. lacustre* in 41.4% of cases and accurately predicted the absence of *R. lacustre* in 98.4% of cases. Overall, the model correctly classified 94.0% of the 1258 plots used to develop the model. The model suggests that wetter sites, riparian and wetland areas, with subalpine fir, Engelmann spruce, and alder comprising a dense overstory are likely habitats for *R. lacustre* in Colorado and central and southeastern Wyoming.

Ribes montigenum

The selected logistic regression model for predicting the odds of occurrence of *R. montigenum* utilized 2 variables: elevation (m) ($p<0.0001$) and the presence or absence of Engelmann spruce ($p=0.003$) (Table 2.8). The logistic regression function is shown in Figure 2.11. The odds of a site containing *R. montigenum* increase by 2 with every 100m increase in elevation and increase by a factor of 3.65 with Engelmann spruce as a dominant overstory component over sites without an Engelmann spruce component. The Kappa statistic (0.655) and the AUC (0.969) indicate the model provides good agreement between actual and predicted occurrence of *R. montigenum*. The model accurately predicted the presence of *R. montigenum* in 64.9% of cases and accurately predicted the

absence of *R. montigenum* in 98.2% of cases. Overall, the model correctly classified 96.2% of the 1256 plots used to develop the model. The model suggests that high elevation sites with Engelmann spruce are likely habitats for *R. montigenum*.

Discussion

The goal of this study was to determine whether or not the alternate hosts for *Cronartium ribicola* are present both within and in the vicinity of native white pine stands and to clarify relationships between site variables and presence and density by *Ribes* species. The *Ribes* species recorded in this study should not be considered a comprehensive list of *Ribes* species present within Colorado and central and southeastern Wyoming; rather this was a study of the *Ribes* species growing within the areas surrounding native white pine populations. *Ribes* species are present in all of the study areas, but the species present and the density of each species varied between the study sites. Species of *Ribes* were found growing across a wide elevational range, 1750 to 3650 m, which encompasses much of the range of white pines in central and southeastern Wyoming and Colorado. *Ribes cereum* and *R. inerme* were present in all of the study areas, while *R. lacustre* and *R. montigenum* were locally prevalent in some study areas and absent from others, and *R. laxiflorum*, *R. hudsonianum*, and *R. viscosissimum* were not common in any of the study areas.

The results of this study are consistent with previous reports; we found that *R. cereum* densities were negatively correlated with elevation and that highest densities occurred in open areas. Peet (1981) reports that *Ribes cereum* is often a dominant shrub species on

the cooler, rockier areas of xeric, low-elevation woodlands along the Colorado Front Range. Van Arsdel and Geils (2004) note that *R. cereum* grows in open areas from low elevation sites (1500 – 2700 m), where it is in greater abundance, to higher elevation sites (2750 – 3650 m) in New Mexico and Colorado. Our attempts to predict the types of sites on which one would be likely to find *R. cereum* occurring were not all that promising (K=0.324); however, the odds of *R. cereum* occurrence increase with increasing slope steepness and the presence of ponderosa pine and decrease with increasing elevation and the presence of lodgepole pine and subalpine fir. While *Ribes cereum* is generally considered among the least susceptible of western North American *Ribes* species to *Cronartium ribicola* and the lowest producer of telia when infected (Kimmey 1938), some forms have been reported to produce significant inocula under conducive infection conditions (Kimmey and Mielke 1944). In several studies of the relative susceptibility of western North American *Ribes* species to *Cronartium ribicola*, it has been shown the partial-shade and shade forms of *Ribes* species are more susceptible to *Cronartium ribicola* and produce more telia than do full sun, or open grown, forms of the same species (Mielke 1943, Mielke et al. 1937). In Colorado and central and southeastern Wyoming, *R. cereum* densities were highest in lower elevation meadow, non-forested, and open sites, all of which are likely to be hotter and drier than other types of sites. This suggests that *R. cereum* may not be growing under the conditions that are most favorable for infection by *C. ribicola* and telial production.

Ribes inerme is a major component of the shrub communities found on cool, northern aspects and ravines where low-elevation woodlands are supplanted by forests (Peet

1981). Van Arsdel and Geils (2004) state that *R. inerme* can be found growing in riparian areas, meadows, and cool, rocky seeps. In general, the results from this study are consistent with these previous reports of *R. inerme* distributions. Our study indicates that densities of *R. inerme* are significantly higher in riparian and wetland areas than any other type. However, we found that *R. inerme* can be found on slopes of all aspects, but that northeastern facing slopes had the highest densities followed closely by eastern, southeastern, and southwestern facing slopes. The odds of *R. inerme* growing on a site increase at lower elevations on sites with components of aspen and willow, both of which are associated with more mesic sites. Of the *Ribes* species found through this survey, *R. inerme* has been shown to have a relatively high susceptibility to *Cronartium ribicola* and a high capacity for telial production (Mielke et al. 1937, Mielke 1943). The higher occurrence and density of *R. inerme* in riparian and wetland areas, sites that are likely to have favorable conditions for infection and intensification of the rust fungus (Mielke 1937), may indicate that *R. inerme* is playing, or may in the future play, an important role in the propagation of *C. ribicola* throughout our study areas. At the spatially isolated Gallinas Peak (Cibola N.F., New Mexico), *R. inerme* is the only *Ribes* species present and is considered responsible for producing an outbreak of white pine blister rust on southwestern white pine (Van Arsdel and Geils 2004).

Ribes lacustre occurs in wetlands, along stream banks, and in cool, moist forests below 2,600 m (Van Arsdel and Geils 2004, Peet 1981). We also found that densities of *R. lacustre* were highest in riparian areas, in valley bottoms, and in forested areas with closed canopies. The odds of finding *R. lacustre* on a site increase on wetter sites with

subalpine fir, Engelmann spruce, and alder comprising a dense overstory. Several studies have indicated that *R. lacustre* is moderately susceptible to *C. ribicola* and that telial production on *R. lacustre* is relatively low (Kimmey 1938, Mielke et al. 1937). However, one area in British Columbia experienced a rapid increase in damage to pines by white pine blister rust that was attributed solely to inoculum production on *R. lacustre*, the only *Ribes* species present in the vicinity of the study area (Mielke 1937). Considering that *R. lacustre* appears to occupy sites likely to have favorable conditions for infection and spore production (i.e. shaded, cool, riparian areas), this species must be considered a potentially important component the white pine blister rust pathosystem.

In the forest-alpine ecotone, *Ribes montigenum* is frequently the dominant shrub species where it grows on open slopes and in spruce-fir communities (Van Arsdel and Geils 2004, Peet 1981). We found that *R. montigenum* densities were highest in forested areas that were characterized by open canopies. *Ribes montigenum* densities were also positively correlated with elevation. The best predictors for presence of *R. montigenum* on a site were elevation and presence of Engelmann spruce. Kimmey and Mielke (1944) reported that *R. montigenum* is moderately susceptible to infection by *Cronartium ribicola* and intermediate in telial production. As such, it must also be deemed a potential substrate for inoculum production at higher elevations.

Mielke (1943) proposed that given enough time, all western North American *Ribes* species possess the potential to produce enough white pine blister rust inocula to cause damage to nearby white pines. Our survey indicates that species of *Ribes* are growing

throughout the range of native white pines in Colorado and central and southeastern Wyoming. Although the species that were commonly found in our study areas vary in their susceptibility and ability to produce inocula, all have been shown in previous studies to be capable of taking part in the life cycle of *C. ribicola*. The role of an individual species in proliferating white pine blister rust in an area may be inconsequential as these species rarely exist individually; we found 2 or more species of *Ribes* within each of our study areas. It is evident from this study that the native white pines of Colorado and central and southeastern Wyoming will not escape infection by *Cronartium ribicola* solely due to the absence of the *Ribes* host.

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Figure 2.1. Location of study areas and *Ribes* survey plots in Colorado.

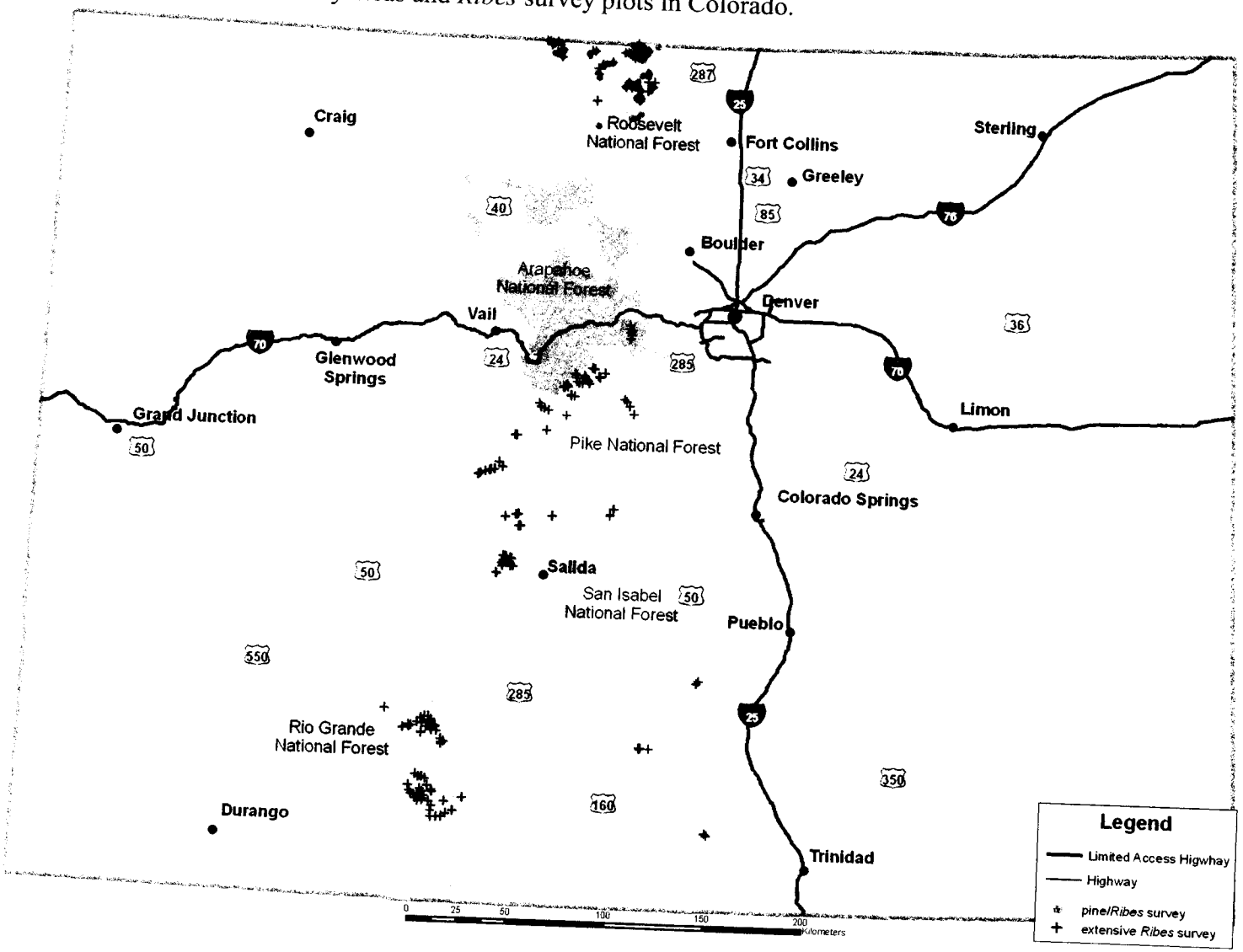


Figure 2.2. Location of study areas and *Ribes* survey plots in Wyoming.

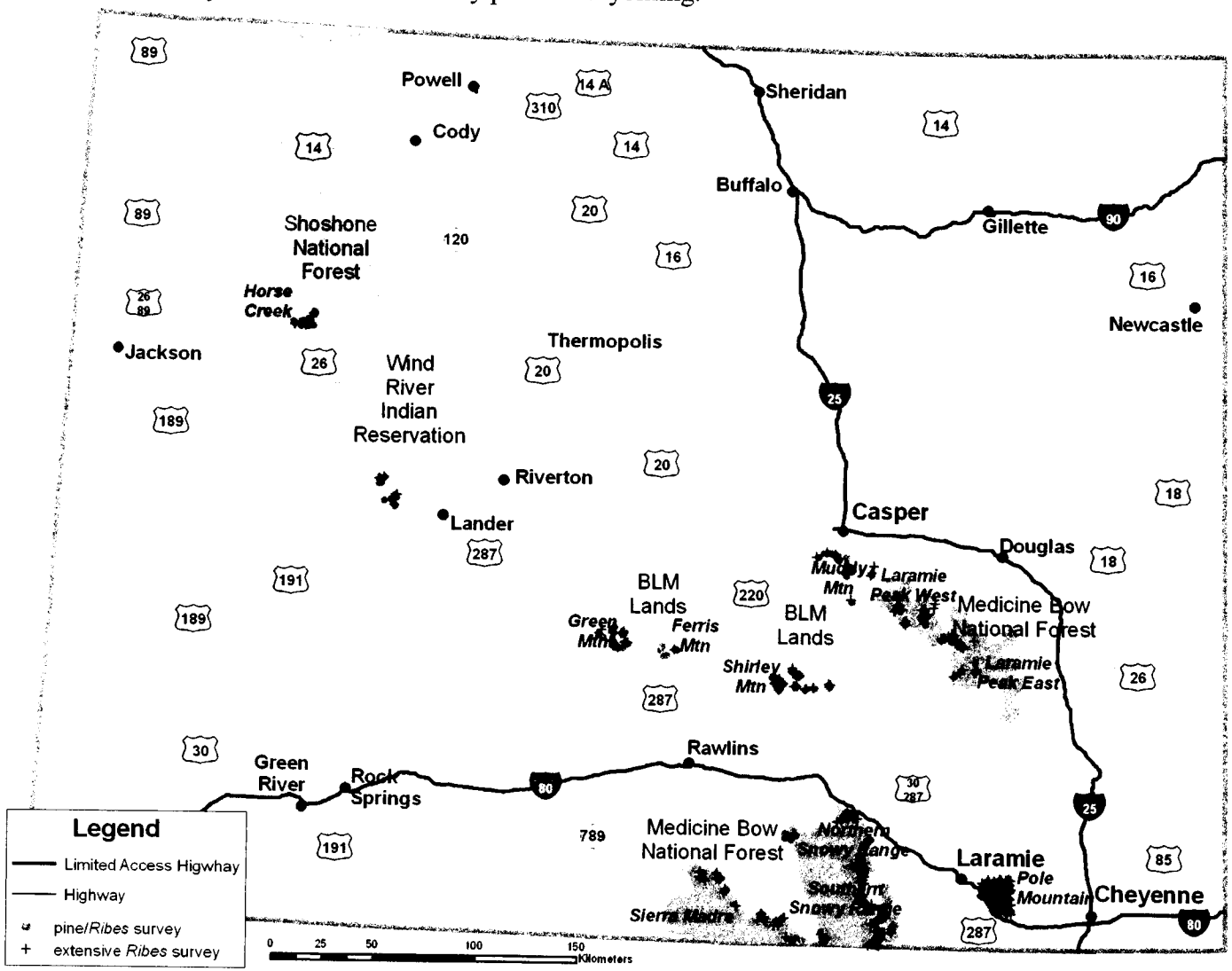
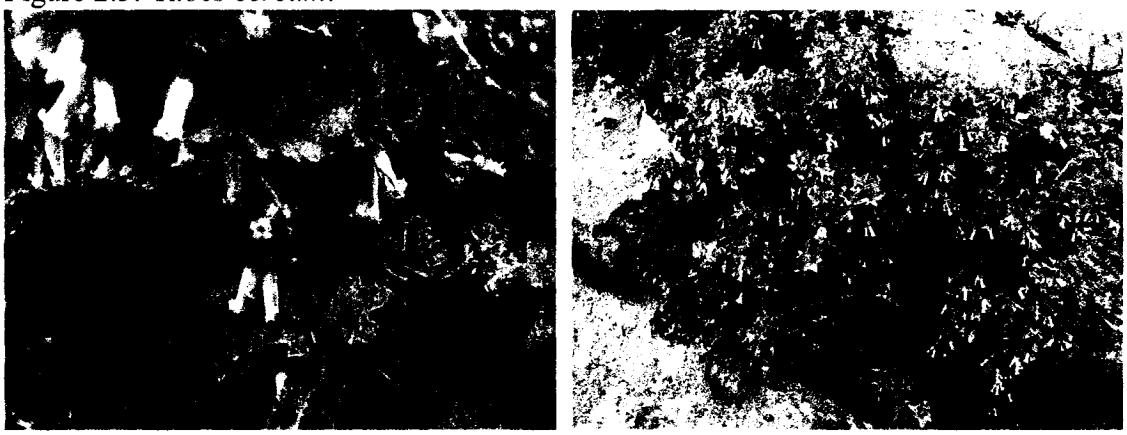
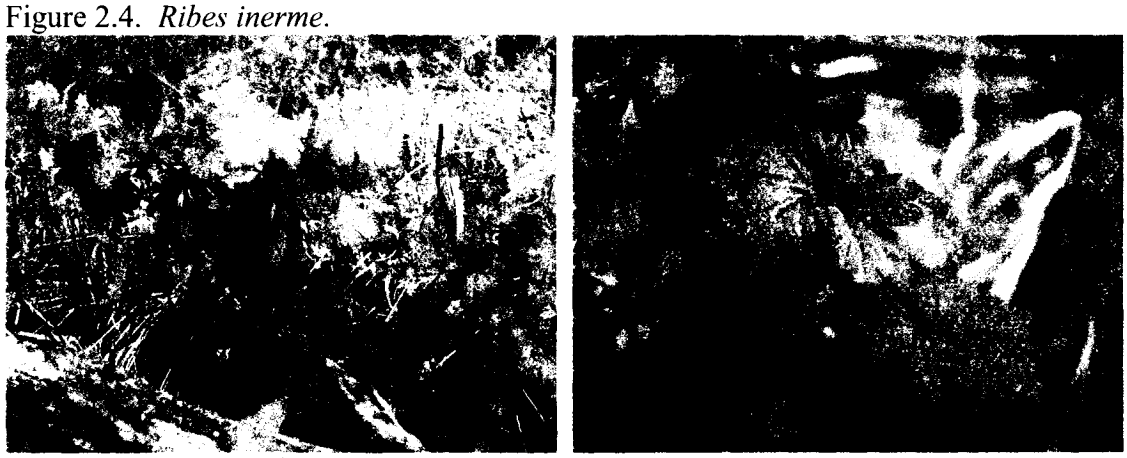


Figure 2.3. *Ribes cereum.*



Photos by Maria Newcomb

Figure 2.4. *Ribes inerme.*



Photos by Maria Newcomb.

Figure 2.5. *Ribes lacustre.*

Photo by Maria Newcomb

Figure 2.6. *Ribes montigenum.*

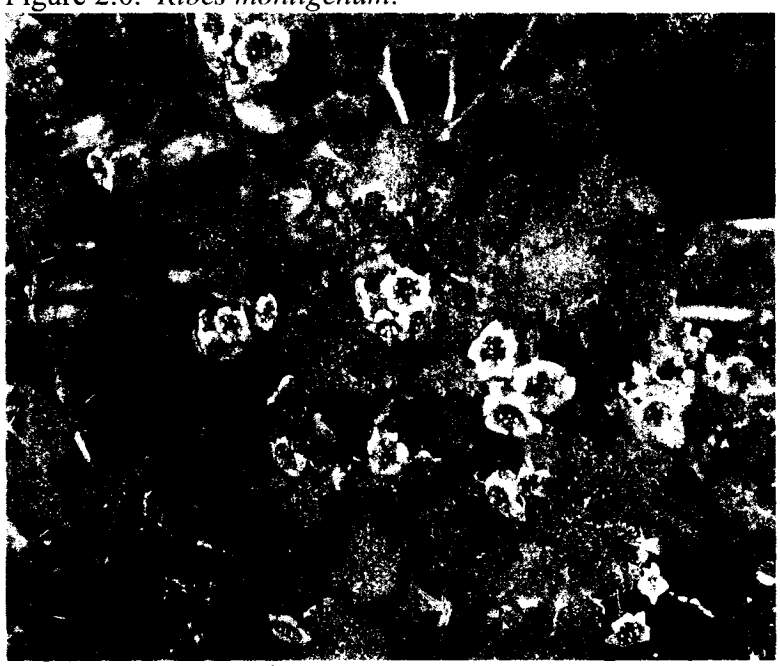
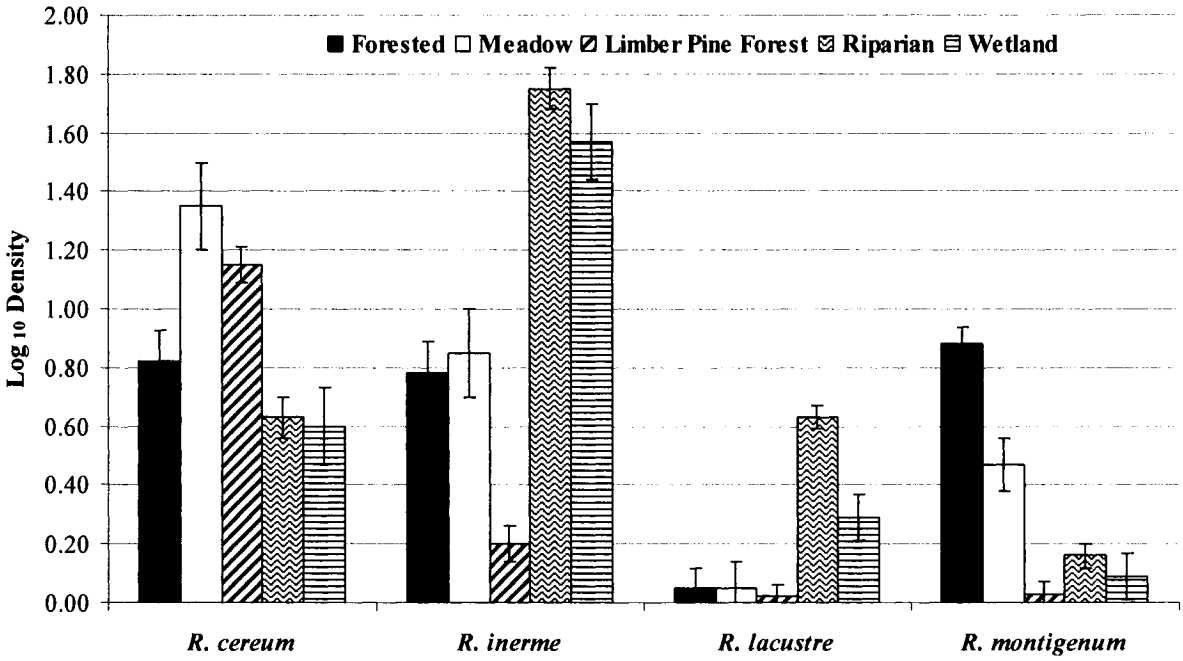


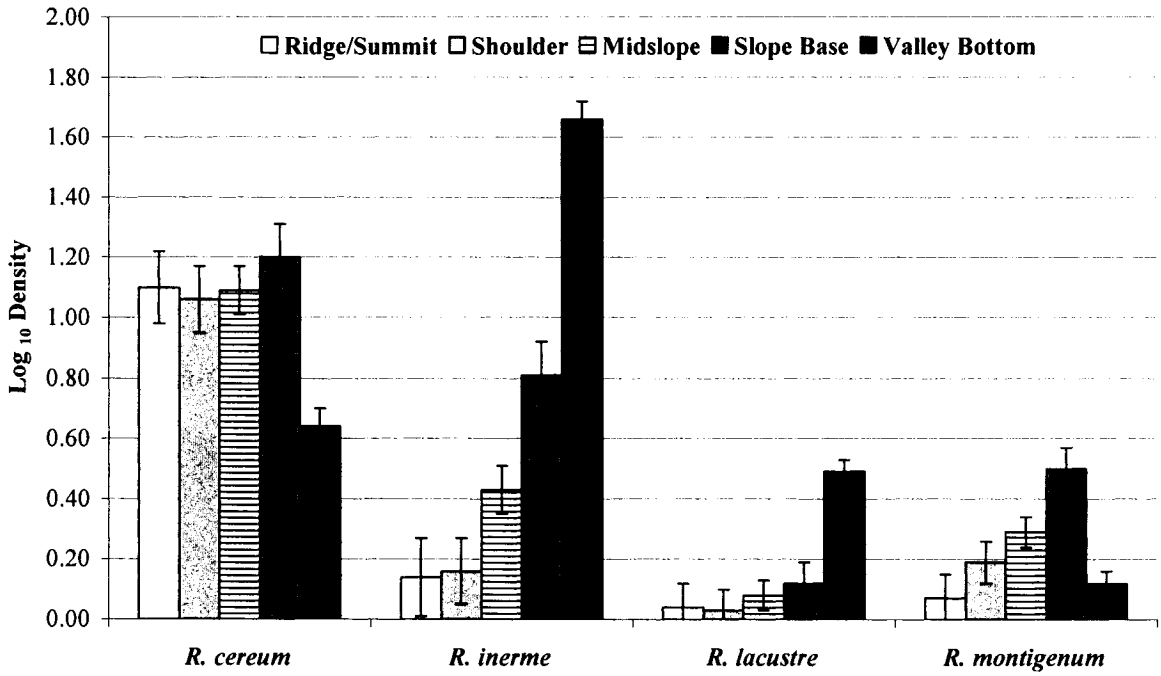
Photo by Maria Newcomb

Figure 2.7. Mean $\log_{10}$ density of 4 *Ribes* species by site description in Colorado and Wyoming.



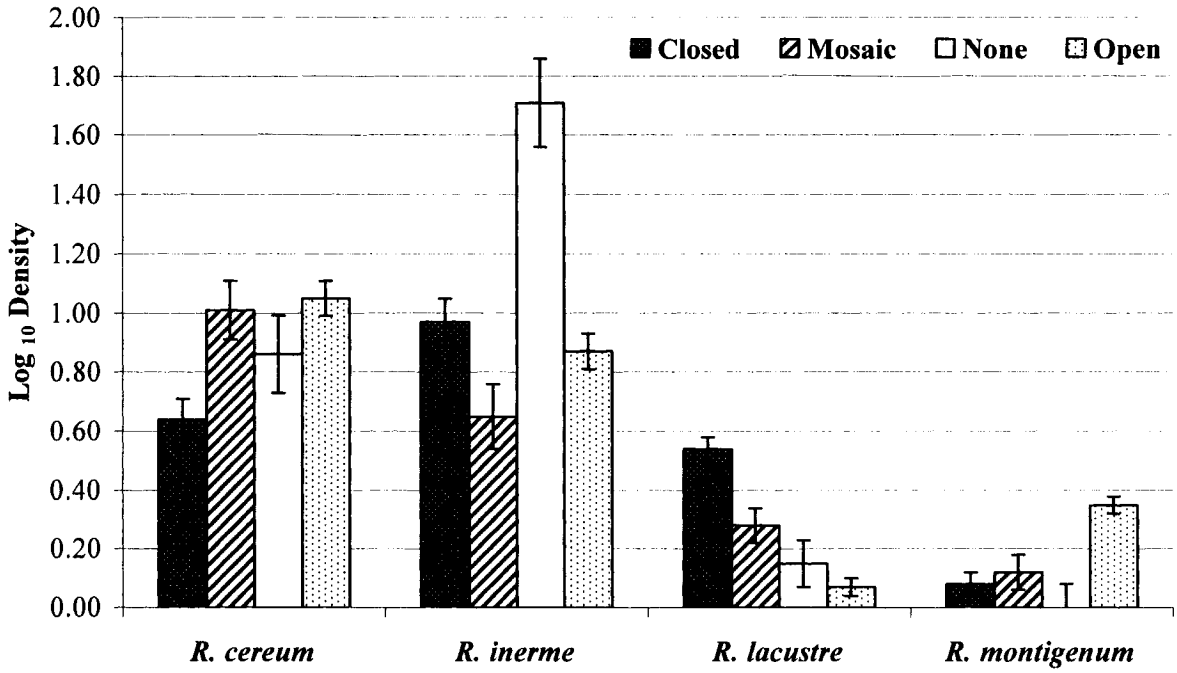
[1] Forested (n=151), Meadow (n=82), Limber pine forest (n=504), Riparian (n=412), Wetland (n=109). Error bars represent +/- 1 standard error of the mean.

Figure 2.8. Mean $\log_{10}$ density of 4 *Ribes* species by slope position in Colorado and Wyoming.



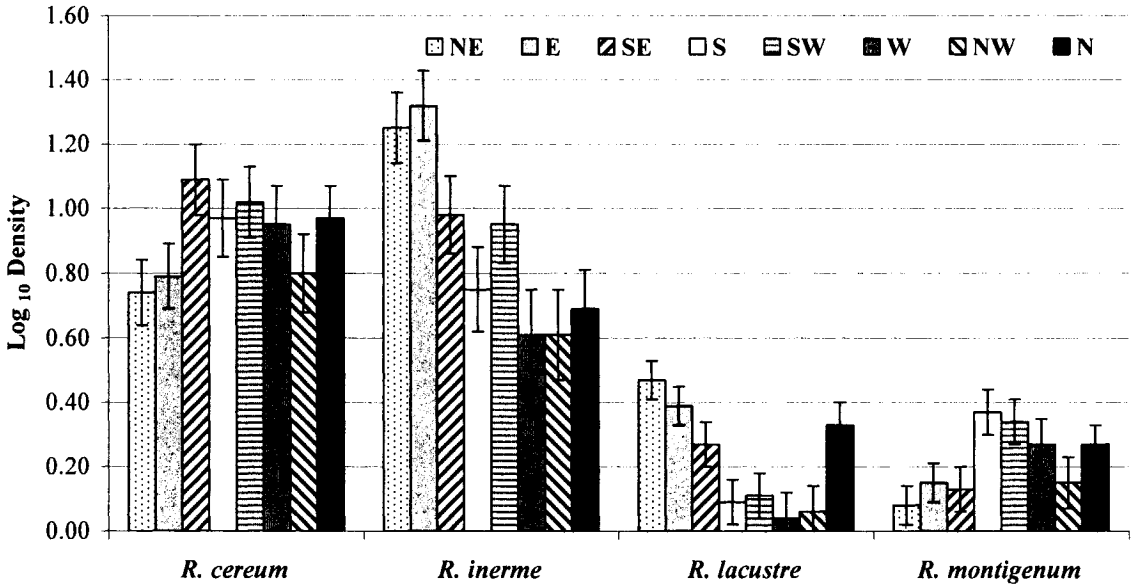
[1] Ridge/Summit (n=118), Shoulder (n=161), Midslope (n=289), Slope Base (n=151), Valley Bottom (n=539). Error bars represent +/- 1 standard error of the mean.

Figure 2.9. Mean $\log_{10}$ density of 4 *Ribes* species by forest stand type in Colorado and Wyoming.



[1] Closed (n=376), Mosaic (n=175), None (n=103), Open (n=596). Error bars represent +/- 1 standard error of the mean.

Figure 2.10. Mean $\log_{10}$ density of 4 *Ribes* species by aspect class in Colorado and Wyoming.



[1] 45°aspect classes (NE 22.5-67.5° (n=197), E 67.5-112.5° (n=202), SE 112.5-157.5° (n=163), S 157.5-202.5° (n=137), SW 202.5-247.5° (n=147), W 247.5-292.5° (n=123), NW 292.5-337.5° (n=118), N >337.5° and <22.5° (n=171)). Error bars represent +/- 1 standard error of the mean.

Figure 2.11. Logistic regression function for probability of occurrence of *Ribes montigenum* illustrating increasing probability of *R. montigenum* with increasing elevation and the presence of Engelmann spruce.

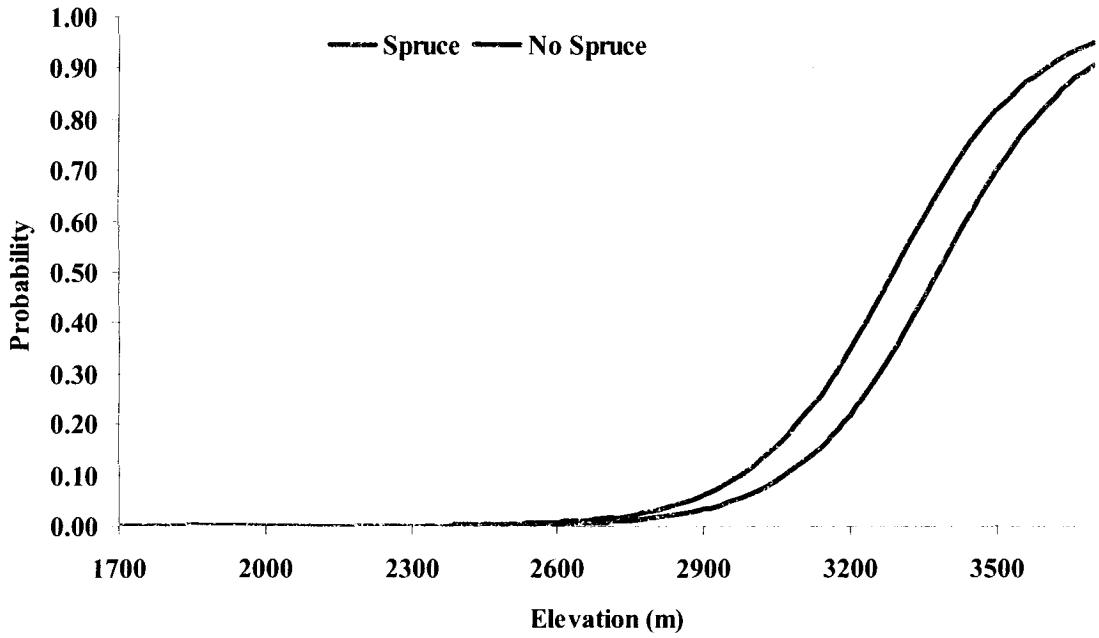


Table 2.1. Distribution and density of *Ribes cereum* in Colorado and Wyoming

Area	Mean $\log_{10}$ Density[a]	S.E.[b]	Occurrence[c]	Elevation[d]
Pole Mountain, WY	1.88 a	0.08	0.68 (154/226)	2307-2834
Wind River Indian Res., WY	1.27 ab	0.26	0.42 (10/24)	2295-2888
Roosevelt N.F., CO	1.19 ab	0.11	0.44 (59/134)	2347-2819
Arapahoe N.F., CO	0.87 bc	0.45	0.25 (2/8)	3018-3231
Snowy Range South, WY	0.86 bc	0.11	0.31 (44/142)	2316-2907
San Isabel N.F., CO	0.81 bc	0.16	0.25 (15/60)	2560-3068
Shirley Mountains, WY	0.81 bc	0.16	0.32 (21/66)	2256-2667
Sierra Madre, WY	0.71 bc	0.15	0.26 (18/68)	2480-2929
Rio Grande N.F., CO	0.59 bc	0.16	0.18 (11/62)	2679-3414
Pike N.F., CO	0.55 bc	0.14	0.17 (13/76)	2861-3231
Green Mountain, WY	0.50 bc	0.18	0.20 (10/51)	2160-2655
Laramie Peak, WY	0.45 bc	0.11	0.19 (25/130)	2112-2597
Muddy Mountain, WY	0.43 bc	0.22	0.16 (5/32)	1884-2467
Snowy Range North, WY	0.42 bc	0.10	0.17 (26/151)	2399-2979
Shoshone N.F., WY	0.24 c	0.24	0.11 (3/28)	2354-2679

[a] Mean $\log_{10}$ m of live stem per $\log_{10}$ ha, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD

[b] Standard error of the mean

[c] Proportion of plots occupied (plots occupied/plots examined)

[d] Elevation range of occupied plots in m (lowest-highest)

Table 2.2. Distribution and density of *Ribes inerme* in Colorado and Wyoming

Area	Mean log_{10} Density[a]	S.E.[b]	Occurrence[c]	Elevation[d]
Pole Mountain, WY	1.57 a	0.10	0.47 (106/226)	2307-2661
San Isabel N.F., CO	1.39 a	0.19	0.43 (26/60)	2560-3506
Pike N.F., CO	1.24 ab	0.17	0.36 (27/76)	2857-3597
Wind River Indian Res., WY	1.20 abc	0.30	0.33 (8/24)	2295-2888
Green Mountain, WY	1.20 abc	0.21	0.35 (13/51)	2160-2655
Shirley Mountains, WY	1.15 abc	0.18	0.33 (22/66)	2256-2508
Roosevelt N.F., CO	1.00 abc	0.13	0.32 (43/134)	2256-2745
Rio Grande N.F., CO	0.91 abc	0.19	0.27 (17/62)	2642-3414
Snowy Range South, WY	0.89 abc	0.12	0.25 (36/142)	2316-2699
Laramie Peak, WY	0.67 abc	0.13	0.25 (33/130)	2102-2569
Shoshone N.F., WY	0.50 abc	0.28	0.18 (5/28)	2370-2679
Snowy Range North, WY	0.28 bc	0.12	0.10 (15/151)	2399-2900
Muddy Mountain, WY	0.26 bc	0.26	0.25 (3/32)	1747-1966
Sierra Madre, WY	0.19 bc	0.18	0.06 (4/68)	2450-2644
Arapahoe N.F., CO	0.14 c	0.52	0.13 (1/8)	2882

[a] Mean log_{10} m of live stem per log_{10} ha, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD

[b] Standard error of the mean

[c] Proportion of plots occupied (plots occupied/plots examined)

[d] Elevation range of occupied plots in m (lowest-highest)

Table 2.3. Distribution and density of *Ribes lacustre* in Colorado and Wyoming

Area[a]	Mean $\log_{10}$ Density[b]	S.E.[c]	Occurrence[d]	Elevation[e]
Snowy Range North, WY	1.02 a	0.07	0.30 (46/151)	2580-3101
Sierra Madre, WY	0.68 ab	0.10	0.24 (16/68)	2479-2893
Snowy Range South, WY	0.35 bc	0.07	0.11 (16/142)	2576-3077
Wind River Indian Res., WY	0.26 bc	0.16	0.08 (2/24)	2824-2888
Laramie Peak, WY	0.20 bc	0.07	0.07 (9/130)	2321-2558
Shirley Mountains, WY	0.15 bc	0.10	0.06 (4/66)	2398-2592
Roosevelt N.F., CO	0.14 bc	0.07	0.04 (6/134)	2603-2862

[a] *Ribes lacustre* was not observed in study areas not listed
[b] Mean $\log_{10}$ m of live stem per $\log_{10}$ ha, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD
[c] Standard error of the mean
[d] Proportion of plots occupied (plots occupied/plots examined)
[e] Elevation range of occupied plots in m (lowest-highest)

Table 2.4. Distribution and density of *Ribes montigenum* in Colorado and Wyoming

Area[a]	Mean $\log_{10}$ Density[b]	S.E.[c]	Occurrence[d]	Elevation[e]
Rio Grande N.F., CO	1.73 a	0.09	0.48 (30/62)	2966-3609
Pike N.F., CO	1.22 a	0.08	0.37 (28/76)	3048-3658
San Isabel N.F., CO	0.56 b	0.09	0.17 (10/60)	3008-3597
Shoshone N.F., WY	0.22 bc	0.13	0.07 (2/28)	2670-2731
Wind River Indian Res., WY	0.15 bc	0.14	0.04 (1/24)	2824
Snowy Range North, WY	0.13 bc	0.06	0.04 (6/151)	2899-3155

[a] *Ribes montigenum* was not observed in study areas not listed
[b] Mean $\log_{10}$ m of live stem per $\log_{10}$ ha, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD
[c] Standard error of the mean
[d] Proportion of plots occupied (plots occupied/plots examined)
[e] Elevation range of occupied plots in m (lowest-highest)

Table 2.5. Results of logistic regression on the odds of *R. cereum* occurrence in Colorado and Wyoming.

					Odds Ratios[b]		
Parameter	**DF**	**Estimate**	**S.E.**	**p[a]**	**Unit**	**Estimate**	**95% C.I.**
Intercept	1	3.313	0.695	<0.0001			
Elevation (m)	1	-0.002	0.000	<0.0001	100	0.84	0.80 0.89
Slope (%)	1	0.040	0.005	<0.0001	1	1.04	1.03 1.05
Ponderosa pine (Present)	1	0.759	0.102	<0.0001		4.57	3.08 6.87
Lodgepole pine (Present)	1	-0.265	0.072	0.0002		0.59	0.44 0.78
Subalpine fir (Present)	1	-0.600	0.108	<0.0001		0.30	0.19 0.46

[a] P-value based on Wald Chi-Square statistic

[b] Likelihood adjusted odds ratios indicate the change in odds that *R. cereum* will occur on a site if the parameter increases by the unit (100m or 1%) or if that parameter present as one of the three dominant tree species on the site.

Table 2.6. Results of logistic regression on the odds of *R. inerme* occurrence in Colorado and Wyoming.

					Odds Ratios[b]		
Parameter	**DF**	**Estimate**	**S.E.**	**p[a]**	**Unit**	**Estimate**	**95% C.I.**
Intercept	1	5.1301	0.815	<0.0001			
Elevation (m)	1	-0.003	0.000	<0.0001	100	0.77	0.72 0.82
Plot Type Riparian	1	0.697	0.167	<0.0001		10.92	6.45 18.90
Plot Type Meadow	1	0.134	0.252	0.5943		6.22	3.14 12.23
Plot Type Forested	1	0.512	0.207	0.0135		9.08	4.97 16.75
Plot Type Wetland	1	0.352	0.206	0.0875		7.74	4.20 14.45
Plot Type Pine/*Ribes*	0	0.000	-	-		-	- -
Lodgepole pine (Present)	1	-0.595	0.091	<0.0001		0.30	0.21 0.43
Aspen (Present)	1	0.291	0.009	0.0017		1.79	1.25 2.58
Subalpine fir (Present)	1	-0.662	0.114	<0.0001		0.27	0.17 0.41
Overstory trees (Present)	1	0.430	0.154	0.0051		2.37	1.30 4.34
Big sage (Present)	1	-0.469	0.122	0.0001		0.39	0.24 0.63
Willow (Present)	1	0.501	0.114	<0.0001		2.73	1.75 4.28

[a] P-value based on Wald Chi-Square statistic

[b] Likelihood adjusted odds ratios indicate the change in odds that *R. inerme* will occur on a site if the parameter increases by the unit (100m), compared to site Limber pine forest, or if that parameter is present as one of the three dominant overstory or understory cover types on the site.

Table 2.7. Results of logistic regression on the odds of *R. lacustre* occurrence in Colorado and Wyoming.

					Odds Ratios[b]		
Parameter	**DF**	**Estimate**	**S.E.**	**p[a]**	**Estimate**	**95% C.I.**	
Intercept	1	-2.002	0.308	<0.0001			
Riparian Plot	1	1.672	0.307	<0.0001	18.49	6.70	65.96
Meadow Plot	1	-0.316	0.843	0.7077	2.53	0.12	18.94
Forested Plot	1	-1.166	0.546	0.0326	1.08	0.20	5.19
Wetland Plot	1	1.055	0.416	0.0111	9.97	2.79	41.19
Plot Type Pine/*Ribes*	0	0.000	-	-	-	-	-
Subalpine fir (Present)	1	0.888	0.143	<0.0001	5.91	3.40	10.44
Alder (Present)	1	0.899	0.173	<0.0001	6.03	3.08	11.97
Engelmann spruce (Present)	1	0.508	0.146	0.0005	2.76	1.56	4.92
Leaf Litter (Present)	1	0.760	0.155	<0.0001	4.58	2.51	8.45

[a] P-value based on Wald Chi-Square statistic

[b] Likelihood adjusted odds ratios indicate the change in odds that *R. lacustre* will occur on a site compared to site Limber pine forest or if that parameter is present as one of the three dominant overstory or understory cover types on the site.

Table 2.8. Results of logistic regression on the odds of *R. montigenum* occurrence in Colorado and Wyoming.

					Odds Ratios[b]			
Parameter	**DF**	**Estimate**	**S.E.**	**p[a]**	**Unit**	**Estimate**	**95% C.I.**	
Intercept	1	-23.800	2.315	<0.0001				
Elevation (m)	1	0.007	0.001	<0.0001	100	2.02	1.77	2.36
Engelmann spruce (Present)	1	0.648	0.221	0.0033		3.66	1.58	9.05

[a] P-value based on Wald Chi-Square statistic

[b] Likelihood adjusted odds ratios indicate the change in odds that *R. montigenum* will occur on a site if the parameter increases by the unit (100m) or if that parameter is present as one of the three dominant overstory tree species on the site.

Appendix 2.1. Mean $\log_{10}$ density of 4 *Ribes* species by site description in Colorado and Wyoming.

		R. cereum		***R. inerme***		***R. lacustre***		***R. montigenum***	
		Mean $\log_{10}$		**Mean $\log_{10}$**		**Mean $\log_{10}$**		**Mean $\log_{10}$**	
Site	**N**	**Density[a]**	**S.E.[b]**	**Density[a]**	**S.E.[b]**	**Density[a]**	**S.E.[b]**	**Density[a]**	**S.E.[b]**
Forested	151	0.82 bc	0.11	0.78 b	0.11	0.05 bc	0.07	0.88 a	0.06
Meadow	82	1.35 a	0.15	0.85 b	0.15	0.05 bc	0.09	0.47 b	0.09
Limber Pine Forest	504	1.15 ab	0.06	0.20 c	0.06	0.02 c	0.04	0.03 c	0.04
Riparian	412	0.63 c	0.07	1.75 a	0.07	0.63 a	0.04	0.16 c	0.04
Wetland	109	0.60 c	0.13	1.57 a	0.13	0.29 b	0.08	0.09 c	0.08

[a] Mean $\log_{10}$ m of live stem per ha, means within species followed by different letters are significantly different at p=0.05 based on Tukey's HSD.

[b] Standard error of the mean.

Appendix 2.2. Mean $\log_{10}$ density of 4 *Ribes* species by slope position in Colorado and Wyoming.

		R. cereum		***R. inerme***		***R. lacustre***		***R. montigenum***	
		Mean $\log_{10}$		**Mean $\log_{10}$**		**Mean $\log_{10}$**		**Mean $\log_{10}$**	
Slope Position	**N**	**Density[a]**	**S.E.[b]**	**Density[a]**	**S.E.[b]**	**Density[a]**	**S.E.[b]**	**Density[a]**	**S.E.[b]**
Ridge/Summit	118	1.10 a	0.12	0.14 c	0.13	0.04 b	0.08	0.07 b	0.08
Shoulder	161	1.06 a	0.11	0.16 c	0.11	0.03 b	0.07	0.19 b	0.07
Midslope	289	1.09 a	0.08	0.43 bc	0.08	0.08 b	0.05	0.29 ab	0.05
Slope Base	151	1.20 a	0.11	0.81 b	0.11	0.12 b	0.07	0.50 a	0.07
Valley Bottom	539	0.64 b	0.06	1.66 a	0.06	0.49 a	0.04	0.12 b	0.04

[a] Mean $\log_{10}$ density in m of live stem per ha, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD.

[b] Standard error of the mean.

Appendix 2.3. Mean $\log_{10}$ density of 4 *Ribes* species by forest stand type in Colorado and Wyoming.

		R. cereum		***R. inerme***		***R. lacustre***		***R. montigenum***	
		Mean $\log_{10}$		**Mean $\log_{10}$**		**Mean $\log_{10}$**		**Mean $\log_{10}$**	
Stand Type[a]	**N**	**Density[b]**	**S.E.[c]**	**Density[b]**	**S.E.[c]**	**Density[b]**	**S.E.[c]**	**Density[b]**	**S.E.[c]**
Closed	376	0.64 b	0.07	0.97 b	0.08	0.54 a	0.04	0.08 b	0.04
Mosaic	175	1.01 a	0.10	0.65 b	0.11	0.28 b	0.06	0.12 b	0.06
None	103	0.86 ab	0.13	1.71 a	0.15	0.15 b	0.08	0.00 b	0.08
Open	596	1.05 a	0.06	0.87 b	0.06	0.07 b	0.03	0.35 a	0.03

[a] Stand Type Descriptions: Closed=crowns of overstory trees touching, understory shaded; Mosaic=containing areas with both open and closed canopies; None=no overstory trees present; Open=crowns of overstory trees not touching, understory exposed to sunlight.

[b] Mean $\log_{10}$ density in m of live stem per ha, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD.

[c] Standard error of the mean.

Appendix 2.4. Mean $\log_{10}$ density of 4 *Ribes* species by aspect class in Colorado and Wyoming.

		R. cereum		***R. inerme***		***R. lacustre***		***R. montigenum***	
		Mean $\log_{10}$		**Mean $\log_{10}$**		**Mean $\log_{10}$**		**Mean $\log_{10}$**	
Aspect[a]	**N**	**Density[b]**	**S.E.[c]**	**Density[b]**	**S.E.[c]**	**Density[b]**	**S.E.[c]**	**Density[b]**	**S.E.[c]**
NE	197	0.74 a	0.10	1.25 ab	0.11	0.47 a	0.06	0.08 a	0.06
E	202	0.79 a	0.10	1.32 a	0.11	0.39 ab	0.06	0.15 a	0.06
SE	163	1.09 a	0.11	0.98 abc	0.12	0.27 abc	0.07	0.13 a	0.07
S	137	0.97 a	0.12	0.75 bc	0.13	0.09 bc	0.07	0.37 a	0.07
SW	147	1.02 a	0.11	0.95 abc	0.12	0.11 bc	0.07	0.34 a	0.07
W	123	0.95 a	0.12	0.61 c	0.14	0.04 c	0.08	0.27 a	0.08
NW	118	0.80 a	0.12	0.61 c	0.14	0.06 c	0.08	0.15 a	0.08
N	171	0.97 a	0.10	0.69 c	0.12	0.33 abc	0.07	0.27 a	0.06

[a] 45°aspect classes (NE 22.5-67.5°, E 67.5-112.5°, SE 112.5-157.5°, S 157.5-202.5°, SW 202.5-247.5°, W 247.5-292.5°, NW 292.5-337.5°, N >337.5° and <22.5°).

[b] Mean $\log_{10}$ density in m of live stem per ha, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD.

[c] Standard error of the mean.

Chapter 3.

Growth rates of white pine blister rust cankers on limber pine in the central Rocky Mountains

Introduction

Since its introduction in 1910 to western North America, *Cronartium ribicola* (J. C. Fisch. ex Rabh.), the pathogen that causes white pine blister rust (WPBR), has spread through many of the West's susceptible white pine populations (Figure 3.1, Samman et al. 2003). Knowledge of the distribution of the pathogen has been derived primarily from non-intensive but spatially extensive detection and scouting trips performed by USDA Forest Service personnel (Benedict 1981, Brown 1967). The pathogen was first reported on *Ribes* in Wyoming, in the vicinity of Yellowstone National Park in the mid-1940s (Brown and Graham 1969, USDA Forest Service 1950, USDA Forest Service 1951). Detection and scouting in Wyoming and Colorado for WPBR were apparently suspended between the mid 1970s and the late 1990s. Since that time, WPBR was recorded in Colorado for the first time in 1998 on the Roosevelt National Forest in the northernmost part of the state (Johnson and Jacobi 2000). More recently, WPBR was discovered in the Wet and Sangre de Cristo Mountains of southern Colorado in 2003, more than 450 km from other known infections (Blodgett and Sullivan 2004). Recent surveys of Wyoming and Colorado limber pines have revealed considerable variation in the levels of infestation (Kearns 2005, Chapter 1).

Any attempt to examine the epidemiology of a specific plant disease must contain a temporal component to determine why there are variations in levels of infestation. Unfortunately, one of the many unknowns for areas impacted by WPBR is determining the length of time the pathogen has been present and how many infection episodes have occurred. Previous studies have indicated that there is a progressive intensification of WPBR with time (Lachmund 1934b, Fracker 1936, Conklin 2004), but we do not know how long it has taken the rust to intensify. Thus, aging WPBR infections would help determine the time since infection and number of infection episodes. Lachmund (1934a) suggested that knowledge of canker growth rates could permit estimation of the temporal development of infections and even reasonably accurate forecasting of the time and extent of damage to the white pine host based on current conditions.

Other researchers have had success using the pattern of canker distribution on interwhorls of western white pine (*Pinus monticola* Dougl.) (Lachmund 1933a) and sugar pine (*P. lambertiana* Dougl.) (Kimmey 1954) to determine the year of initial infection. However, limber pine (*P. flexilis* James), the focus of this study, maintains its needles for much longer periods of time, for 10 years (Schoettle and Rochelle 2000) and occasionally up to 12 years (Kearns, unpublished data), which could potentially provide a larger target of interwhorls and associated needles for infection. The aging of interwhorls limits information on the time of infection to those cankers that can be attributed to a specific interwhorl for the initiation of infection. This eliminates cankers that are older, larger, and that entered the main branch or stem from side branches from the analysis. Also, with this interwhorl aging strategy reconstructing potentially 40 years of infection

episodes would be nearly impossible. As such, the aging of interwhorls with cankers was deemed insufficient to determine the initiation of infection. Instead, we hypothesized that we could use canker length as a surrogate for estimating the duration of infestation and number of infection episodes in limber pine in the central Rocky Mountains.

Several researchers have examined canker growth rates in commercially important white pine species, including western white pine (Harvey 1967, Slipp 1951, Lachmund 1934a) and eastern white pine (*P. strobus* L.) (Phelps and Weber 1969, Rhoads 1920). In all cases, the researchers were able to develop canker growth rate models that provided a measure of annual canker growth. No such studies have been conducted in limber pine. Thus, the objectives of this study were 1) to record canker lengths on limber pine in white pine blister rust infested areas, 2) determine the relationship between canker length and time since infection, and 3) to create a canker growth rate model that would allow investigators to estimate the length of time that the pathogen has been infecting limber pines in an infested area.

Methods

Study areas

Surveys for white pine blister rust occurred on 13 study areas in central and southeastern Wyoming and northern Colorado. Study areas were defined by government management units and geographical features (Figure 3.2) and included: the Horse Creek area of the Shoshone National Forest, Wyoming; Wind River Indian Reservation, Wyoming lands managed by the Bureau of Indian Affairs (BIA); Green Mountain, Ferris Mountain,

Shirley Mountains, and Muddy Mountain, Wyoming lands managed by the Bureau of Land Management (BLM); Laramie Peak East and West sections, Sierra Madre, North and South sections of the Snowy Range, and Pole Mountain areas of the Medicine Bow National Forest, Wyoming; and the Canyon Lakes District of the Roosevelt National Forest, Colorado.

Stand selection

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 (RMRIS) database. Digital Ortho Quadrangles were obtained from the Roosevelt and Medicine Bow National Forests and maps created to direct the sampling effort in these areas. Post-stratification 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, on all aspects, topographic positions, and forest composition types available for sampling. Surveyed stands were within 3 kilometers of a road to limit travel time between stands and maximize the number of plots established. Paper maps were obtained for areas managed by Bureau of Land Management and Bureau of Indian Affairs. Surveys in non-Forest Service managed areas were directed to locations recommended by employees familiar with the areas as having significant populations of limber pine.

Canker Length Survey

Limber pine stands were sampled by belt transects. A plot consisted of two to five pine transects with the goal of examining at least 30 limber pines in each series of transects. Transects were 61 x 4.6 m and were located along random bearings through the stand. The GPS coordinates of the starting point of each transect were recorded. Two trained observers used binoculars to examine the crowns of trees for cankers and other damages. 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. Lengths of live (active) WPBR cankers were recorded when they were present. Cankers were considered active when any macroscopic indication of live fungus (discoloration, sporulation) was evident. Whenever feasible, canker lengths were measured, but when cankers were present in the upper crowns of trees, their lengths were visually estimated. In the summer of 2002, within infested plots up to four canker lengths were recorded on 10 randomly selected trees. Both the minimum and maximum canker lengths recorded as well as two intermediate canker lengths with the objective of recording the variety of canker lengths present. In the summers of 2003 and 2004, complete counts and canker lengths were recorded for all active WPBR cankers present on at least 10 infected limber pines encountered in transects. Branch canker size was estimated by measuring the total length of swelling, rodent chewing, blistering, sporulation, discoloration, or other external evidence of a canker. For stem cankers, total canker size was estimated as described above for branch cankers plus the total length of originating branch canker. Trees that

were classified as old dead were not evaluated for cankers, due to the deterioration of these trees. Using these methods 504 plots were established in 2002-2004.

Canker Collections

Collections were made of live cankers from 4 study areas from April through September 2003: Shirley Mountains, Muddy Mountain, and Pole Mountain areas, Wyoming, and the Roosevelt National Forest, Colorado. Elevations of collection sites ranged from 2290 to 2895 m. Cankered branches were removed where they met the stem, and cankered stems were cut 60 to 90 cm below the canker margin. For each tree from which cankers were collected the following data were recorded: diameter class (<5 cm, 5.1 – 15.4 cm, 15.5 - 30.5 cm, >30.5 cm diameter at breast height (DBH = 1.37 m)), crown class, live crown (%), height, and any other damages present. For each canker, the type (branch or stem), distance to bole, branch height and canker center height were recorded. At each site on which cankers were collected, the elevation, GPS coordinates, slope percent, slope aspect, slope position, slope configuration, stand structure, and the three most common overstory and understory cover types were recorded. Using these methods 150 WPBR branch and stem cankers were collected.

Cankers were transported to the lab where total canker length based on external visual evaluation, diameter at canker center, diameter of the branch or stem below the canker (proximal diameter), proximal and distal canker lengths were recorded. The extent of the zone of bark discoloration was used as the basis for total canker length. Krebill (1968) reported that in *Cronartium ribicola* cankers in western white and limber pines the

leading edge of the fungal hyphae was less than 1 cm beyond visible bark discoloration. Canker center was established where the bark cracking patterns indicated the oldest affected area. A band saw was used to cut cross-sections through canker center and at the base of the stem or branch to provide an unaffected baseline for tree ring comparisons. Cross-sections were then examined using a binocular dissecting microspore. Crossdating, conducted using the skeleton plot technique (Stokes and Smiley 1968) based on chronologies developed from cross-sections from the base of each cankered branch or stem, was utilized to determine the year of the first incomplete ring formed at canker center. The number of partial or incomplete rings formed at canker center and the year in which an orange stain was first evident in the cross-section were also recorded.

Data Analyses

All statistical analyses were performed utilizing SAS (version 9.1, SAS Institute Inc.) statistical program. Tukey's honest significant difference (HSD) was used for multiple comparisons of means because it is recommended for unequal sample sizes and is considered conservative in that it has a low type I error rate (falsely rejecting the null hypothesis) and shows fewer significant differences such that variables are more likely to be useful in model building (P. Chapman, pers. comm.). The Proc GLM (General Linear Model) module, assuming a Gaussian distribution, was used to develop the canker growth rate model as both continuous and categorical variables were employed.

Slipp (1951) reported in his study of WPBR canker growth rates in western white pine that an average of 20% of the canker's annual growth occurred from October through

April, a period generally considered outside the host tree's growing season. Lachmund (1934a) found in western white pine that 15 to 17% of annual canker growth occurred during the winter. Kimmey (1940), working in sugar pine, found that approximately 80% of total canker growth occurred from May 1 through October. In order to account for the different times during the growing season of 2003 that we collected cankers, we considered cankers collected in April to have had 0.2 of the 2003 growing season, those collected between May 15 and June 15 to have 0.36, between June 16 and July 15 to have 0.52, between July 16 and August 15 to have 0.68, and those collected between August 16 and September 30 to have 0.84 of the growing season. Number of years dead at canker center was determined by subtracting the year of the last complete ring formation (first year with an incomplete annual ring less one year) from the time that the canker was collected. For example, a branch canker collected on June 20, 2003 with the first incomplete ring formed in 1998, would have been dead at canker center for 6.52 years (2003.52 – (1998-1)).

Maximum longitudinal canker growth rate was then calculated as the total canker length divided by the number of years dead. This rate was considered a maximum potential rate because the progression from visible, external symptoms of cankers to cambial death would take a minimum of 1 year and may take considerably longer. In western white pine, the period of time between needle infection and the appearance of bark discoloration ranged between 10 and 41 months (Lachmund 1933b). Following this incubation period, the production of pycniospores takes another 1 to 10 months. Then, after another 6 to 30 months aeciospores are produced in the area that previously

produced pycniospores (Lachmund 1933b). It is the production of these aeciospores that disrupts the bark and likely causes the cambial death that we have analyzed as incomplete ring formation. While, no such information is available for limber pine, we assumed that the length of time between the first appearance of the canker and disruption of the cambium was 7 to 40 months. We used 1 year for all samples, which represents a minimum period of time between external evidence of a canker and disruption of the cambium. The proximal canker (toward the main stem) growth rate was calculated as the proximal canker length, or distance from canker center to the proximal edge of external canker symptoms, divided by the number of years dead. Circumferential growth rates were calculated by dividing the circumference at canker center by the number of years it took to girdle the branch or stem (number of partial rings formed).

Results

Canker length survey

Of the 504 survey plots established, canker length data were collected on 258 plots. The number of canker lengths recorded per plot ranged from 1 to 239 and averaged 14. Recorded cankers ranged in length from 1.3 to 213.4 cm with the largest cankers recorded at the Green Mountain study area. Mean maximum canker lengths varied significantly by site (Table 3.1). The longest average maximum canker lengths were recorded on the Laramie Peak West study area at 91.9 cm (standard error (SE) 11.7), and the smallest mean maximum canker lengths were recorded on the Southern Snowy Range study area at 10.2 cm (SE 17.3). Average median canker lengths also varied significantly by study area (Table 3.2). The Laramie Peak West and Laramie Peak East study areas

had significantly longer mean median canker lengths than did any other study areas. Both maximum and median canker length were significantly positively correlated with incidence, the number of infected limber pine/number of evaluated limber pine, and two measures of disease severity, the number of cankers (including both branch and stem cankers) per infected limber pine and the number of stem cankers per infected limber pine (Table 3.3).

Canker Collections

One hundred and thirty nine cankers ranging in length from 6 to 123 cm were analyzed. Of these cankers, crossdating was possible on 134 cankers. The 134 cankers that made up our sample had a mean total length of 37.1 cm (SE 2.1). The majority, 112 of 134 (83.6%), were branch cankers, with 22 (16.4%) stem cankers also analyzed. Diameters at canker center, as measured outside the bark, ranged from 1.1 to 11.6 cm and averaged 3.6 cm (SE 0.1). Diameters at the proximal end of the canker, the end closest to the bole or the ground for branch and stem cankers, respectively, which were beyond any swelling caused by WPBR infection, ranged from 0.1 to 15.2 cm and averaged 3.3 cm (SE 0.2 cm).

Total canker length was strongly negatively correlated with the first year in which an incomplete ring was formed at canker center (Pearson correlation coefficient (r) = -0.748, $p<0.0001$). Total canker length was positively correlated with number of years dead (r = 0.756, $p<0.0001$) and the number of partial rings formed at canker center (r = 0.475, $p<0.0001$). The number of years dead at canker center alone explained 57% of the

variance in total canker length ($F = 176.08$, $p<0.0001$, numerator degrees of freedom (ndf) = 1, denominator degrees of freedom (ddf) = 132, $R^2 = 0.572$). These data provide evidence of a relationship between canker length and time. Total canker length was positively correlated with proximal branch/stem diameter ($r = 0.767$, $p<0.0001$) and diameter at canker center ($r = 0.706$, $p<0.0001$). Total canker length was weakly correlated with canker center height ($r = 0.235$, $p=0.010$). Total canker lengths were not correlated with distance to the bole, tree height, branch height, or percent live crown.

An orange stain that appears to be a resin-like deposit (Figure 3.3) was present in 85% (114 of 134) of cankers analyzed. The first year in which the orange stain was visible within the annual rings at canker center was strongly negatively correlated with total canker length ($r = -0.810$, $p<0.0001$). The year in which the orange stain was first evident alone explained 66% of the variance in total canker length ($F = 213.18$, $p<0.0001$, ndf = 1, ddf = 112, $R^2=0.656$). The orange stain appeared an average of 1.75 (SE 0.1) years before the first incomplete ring was formed at canker center.

Similar relationships exist between proximal canker length and the first year in which an incomplete ring was formed at canker center ($r = -0.764$, $p<0.0001$) and the first year in which an orange stain was visible within the annual rings at canker center ($r = -0.798$, $p<0.0001$), the number of years dead ($r = 0.771$, $p<0.0001$) and the number of partial rings formed at canker center ($r = 0.413$, $p<0.0001$). Distal canker length was negatively correlated with the first year in which an incomplete ring was formed at canker center ($r = -0.561$, $p<0.0001$) and the first year in which an orange was visible within the annual

rings at canker center ($r = -0.709$, $p<0.0001$), and positively correlated with the number of years dead ($r = 0.570$, $p<0.0001$) and the number of partial rings formed at canker center ($r = 0.453$, $p<0.0001$).

Maximum longitudinal canker growth rate

Total maximum longitudinal canker growth rate, a measure of annual growth both up and down a branch or stem, ranged from 2.2 to 27.2 cm/yr and averaged 8.4 cm/yr (SE 0.4). Total maximum longitudinal canker growth rates were positively correlated with branch/stem diameter at canker center ($r = 0.330$, $p<0.0001$). There were significant differences in canker growth rates by proximal diameter class (Figure 3.4, Appendix 3.1). Cankers on branches and stems in the smallest diameter classes, 0.0 – 1.7 cm and 1.8 – 2.4 cm, had significantly lower mean maximum longitudinal canker growth rates at 6.7 and 7.0 cm/yr, respectively, than did those in the largest diameter class, greater than 4.5 cm, with a mean growth rate of 10.1 cm/yr. However, correlations between longitudinal canker growth rates and proximal diameter were fairly weak ($r=0.276$, $p=0.0013$) and proximal diameter class explained only 9.5% of the variance associated with total longitudinal growth rates ($F = 3.38$. $p=0.0115$, $ndf = 4$, $ddf = 129$, $R^2 = 0.095$).

Total maximum longitudinal canker growth rates were not related to diameter class, height, health status, crown class, or percent live crown of the tree from which the cankers were obtained, nor were longitudinal canker growth rates related to the canker's distance from the bole or the height of the canker. There was a slight, negative correlation between canker growth rate and height of the branch from which it was

collected (r = -0.237, p=0.020). There were significant differences in longitudinal growth rates between stem and branch cankers. Stem cankers had a significantly greater mean growth rate of 10.5 cm/yr (SE 0.9) compared to the average growth rate of 8.0 cm/yr (SE 0.4) for branch cankers based on Tukey's HSD at alpha=0.05. Stem diameters ranged from 1.4 to 15.2 cm and averaged 5.0 cm (SE 0.7). Branch diameters ranged from 0.1 to 9.9 cm and averaged 3.0 cm (SE 0.14). The difference in diameter between stems and branches was significant at alpha=0.05 based on Tukey's HSD. There were also significant differences in annual total longitudinal canker growth based on the condition of the stem/branch beyond the canker. For those stems/branches on which the portion distal (away from stem) to the canker remained alive, mean growth rates were 10.1 cm/yr (SE 0.6), which was significantly greater than the mean growth rate of 7.4 cm/yr (SE 0.4) on stem/branches for which the portion distal to the canker was dead (Figure 3.5, Appendix 3.1). There were also significant differences in mean proximal (toward stem) branch/stem diameter between those with the portion distal to the canker alive (2.5 cm, SE 0.28) and those for which the portion distal to the canker was dead (3.8 cm, SE 0.22).

Proximal canker growth rates

Proximal longitudinal growth rate, a measure of annual growth toward the stem for branch cankers and down the stem for stem cankers, ranged from 0.1 to 13.1 cm/yr and averaged 4.9 cm/yr (SE 0.2) and distal growth rates averaged 3.5 cm/yr (SE 0.2). Proximal longitudinal growth rates were positively correlated with branch/stem diameter at canker center (r = 0.263, p=0.0021) and branch/stem diameter proximal to the canker (r = 0.257, p=0.0028). Although proximal canker growth rates exhibit a trend of increasing

with larger proximal branch/stem diameter, the differences were not statistically significant at alpha=0.05 based on Tukey's HSD (Figure 3.6, Appendix 3.2). Proximal branch/stem diameter explained only 6.6% of the variance in proximal canker growth rates ($F = 9.29$, $p=0.0028$, $ndf = 1$, $ddf = 131$, $R^2 = 0.066$).

Proximal canker growth rates were not related to the diameter class, height, health status, crown class, or percent live crown of the tree from which the cankers were obtained, nor were proximal canker growth rates related to the canker's distance from the bole or the height of the canker. There was a slight, negative correlation between canker growth rate and height of the branch from which it was collected ($r=-0.251$, $p=0.0137$). Stem cankers did not exhibit a significantly greater proximal growth rate (5.7 cm/yr, SE 0.5) than did branch cankers (4.7 cm/yr, SE 0.2). There were significant differences in mean proximal growth rates between cankers growing on stems/branches for which the portion distal to the canker was still alive at 5.8 cm/yr (SE 0.3) and those growing on stems/branches for which the portion distal to the canker was dead at the time of collection, which had a mean proximal growth rate of 4.3 cm/yr (SE 0.3).

Circumferential canker growth rates

For these analyses, only those cankers for which the portion distal to the canker was dead, indication that the branch/stem had been completely girdled by the canker, were used. The mean number of years to girdle all 84 branches and stems was 2.4 (SE 0.2) and ranged from 1 to 9. The number of years to girdle was significantly correlated with the diameter at the center of the canker ($r = 0.452$, $p<0.0001$). The average rate of

circumferential canker growth was 6.5 cm/yr (SE 0.4) and ranged from 1.4 to 18.8 cm/yr. Mean circumferential growth rate was significantly greater for stem cankers (8.8 cm/yr, SE 0.9) than for branch cankers (6.1 cm/yr SE 0.4) based on Tukey's HSD. Circumferential canker growth rates were not related to the diameter class, health status, crown class, percent live crown, or height of the tree from which the canker was collected nor were they related to the canker's distance from the bole, the canker height, or the branch height.

Canker growth rates and site

Relationships between site variables and canker growth rates were explored. There were no significant differences among total longitudinal growth rates or proximal growth rates and the study site from which the canker were collected. The elevation and aspect of the site from which cankers were collected were not related to total maximum canker growth rates or proximal canker growth rates. Cankers collected from sites described as being located at the bottom of slopes, including foot and toe slopes and valley bottoms had significantly greater mean total longitudinal canker growth rates (9.9 cm/yr, SE 0.6, n = 47) and proximal canker growth rates (5.6 cm/yr, SE 0.3, n = 47) than did those described as located along slope shoulders (6.3 cm/yr, SE 0.6, n = 44 and 3.8 cm/yr, SE 0.4, n = 44, respectively).

Canker growth rate models

The only variables that were included in the total longitudinal branch canker growth rate model were branch diameter below the canker, the condition of the branch distal to the

canker, and the branch height. These variables explained 44% of the variability in total longitudinal growth rates found in this study ($F = 13.69$, $p<0.0001$, $ndf = 5$, $ddf = 87$, $R^2 = 0.437$). The model for branches with portions distal to the canker dead is rate = $2.42 + 2.46PD - 0.19PD^2 - 0.36BH$ where PD is proximal diameter of the branch in cm and BH is the height of the branch in m. The model for branches with portions distal to the canker alive is rate = $10.54 + 2.46PD - 0.19PD^2 - 2.13BH$ where PD and BH are as defined above. The growth rate model curves are shown in Figure 3.7 at the mean branch height of 2.15m found in this study.

Approximate period of infestation

Our findings of significant relationships between total canker length and time, and the lack of significant differences between canker collection sites and total longitudinal canker growth rates permits the application of the models herein to canker length data collected throughout the course of this study. Table 3.4 shows the range of time that *Cronartium ribicola* has been infecting limber pines in each of our 13 study areas as of 2003, based on the mean, maximum (mean plus 1 standard deviation (SD)), and minimum (mean minus 1 SD) longitudinal canker growth rates found in this study. This range should be used with caution: only active cankers were recorded and analyzed in this study and no branch diameters were recorded with the recorded canker lengths. According to Kimmey (1969), 62% of all stem cankers were inactive in his survey of western white pine in the Inland Empire, which he attributed to both canker age and the presence of the canker parasitizing fungus *Tuberculina maxima* (Rostr.). As such, our sample of active cankers may underestimate the length of time the pathogen has been

affecting the limber pines on these sites. Even so, these approximate years of infestation should assist in the creation of models that assess risk to native limber pine populations over time.

Discussion

The significant positive correlation between total canker length and number of years dead at canker center supports our hypothesis that canker length is related to the amount of time the pathogen has been infecting the host tree. That there are significant differences in mean maximum and median canker lengths between study areas and significant relationships between incidence and severity of white pine blister rust and maximum and median canker lengths provides support for a link between canker length and the period of time the pathogen has been established and affecting the white pine populations within these study areas. Conklin (2004) reported, in an outbreak of WPBR in New Mexico, that incidence, as measured by proportion of trees infected, increased an average of 2.6% per year. Lachmund (1934b) also provided evidence that both incidence and mortality of western white pine in British Columbia increased with increasing time since infection. Fracker (1936) compiled the results from annual surveys of WPBR plots from various locations across North America. In all cases, there was a continual increase in proportion of trees infected with time. In the northeastern United States, this increase occurred regardless of varying weather conditions, leading Fracker to conclude that once the pathogen is established on a site, intensification is constant and unavoidable. While conditions in western North America may not be as conducive for infection by the

pathogen, with time there appears to be an inevitable increase in the amount of infection that occurs.

The presence of an orange stain in the annual rings in 85% of evaluated cankers and its strong relationship to total canker length is interesting. This orange stain may be evidence of the tree's response to attack by the pathogen. The fact that it first appears an average of 1.75 years prior to incomplete ring formation lends support to this hypothesis. Shigo (1984) recounts that tree-invading fungi, including canker-causing fungi, have been known to result in the formation of a cellular and chemical boundary layer as the tree and pathogen interact. This boundary layer is often discolored and allows determination of the year in which the wound or pathogen attack occurred. Slash pine seedlings (*Pinus elliottii* var. *elliottii*) inoculated with other rust fungi, *Cronartium strobilinum* and *Cronartium quercuum* f. sp. *fusiforme*, produced an initial response zone that was evident due to the presence of a staining, dark pigment (Shukla et al. 2001, Miller and Cowling 1977, respectively). Lundquist and Miller (1984), also working on slash pine seedlings infected with *Cronartium quercuum* f. sp. *fusiforme*, reported the occurrence of an orange pigment that was associated with the production of an impermeable cell layer that effectively cut off infected cells from water and nutrients provided by healthy cells. Krebill (1968) reported that factors including widened rays, haustoria, and hyphae of *Cronartium ribicola* serve as a record for when infection occurred at the cambium as they become imbedded in the annual rings. Our study was not of a histological nature, but the presence of the macroscopically visible orange stain

has the potential for application in the reconstruction of WPBR infestation history as it may indicate infection prior to formation of the canker and the first incomplete ring.

Total longitudinal canker growth rates averaged 8.4 cm/yr in this study and were related to diameter class of the cankered stem/branch, canker location (stem or branch), and the condition of the branch or stem beyond the canker. Lachmund (1934a) observed a significant relationship between longitudinal canker growth rates in *Pinus monticola* and branch and stem size. Lachmund (1933a) reported longitudinal growth rates of 6.3 to 7.6 cm/yr on small diameter (<0.6 cm) western white pine branches and rates of 17.8 to 20 cm/yr on branches and stems greater than 7.6 cm in diameter. In another study of WPBR canker growth in western white pine, Lachmund (1934a) found that branches classified as having poor vigor, as determined by general condition and slow active growth, that averaged 1.1 cm in diameter had a mean longitudinal grow rate of 7.8 cm/yr. Under optimal environmental conditions for growth of western white pine, maximum longitudinal canker growth averaged between 22.9 and 25.4 cm/yr. We had canker growth rates that approached these maximums, but our overall mean longitudinal expansion rate was much less and corresponded to growth rates in less vigorous and smaller diameter western white pine branches. Our lesser canker expansion rates may be related to the less than optimal conditions under which limber pines grow throughout this study area relative to the conditions in British Columbia where Lachmund's studies were conducted. Rhoads (1920) reported a mean longitudinal stem canker growth rate of 12.7 cm/yr in eastern white pine (*Pinus strobus* L.) growing in Maine. Growth rates varied by diameter class, with the smallest class (0.25 – 1.3 cm) averaging 5.3 cm/yr and the largest

diameter class (7.9 – 10.2 cm) averaging 17.7 cm/yr (Rhoads 1920). Stem canker growth rates in eastern white pine in Wisconsin and Minnesota were examined by Phelps and Weber (1969) who reported that rates declined with increasing diameter. The average longitudinal growth rate for stem cankers on 2.5 to 10 cm stems was 10.7 cm/yr which was higher than the 7.1 cm/yr average growth rate on stems 20.6 to 25.4 cm in diameter (Phelps and Weber 1969). In branches 10 cm or greater in diameter, Lachmund (1934a) found that canker growth rates level out to a constant rate. Our canker growth rate modeling efforts also indicate a decline in growth rates for branches greater than about 7.0 cm in diameter.

Longitudinal canker growth rates in limber pine differed significantly between stem and branch cankers. However, it is impossible to separate the effects of diameter from those of canker location, and the significant differences in longitudinal canker growth rate found in this study may be an artifact of the significantly greater diameters of the stems analyzed here. Neither Kimmey (1940) nor Lachmund (1934a) reported significant differences between the growth rates of branch and stem cankers in western white pine. Although tree trunks are generally considered conducive to greater canker growth rates due to their greater growth rate and vigor, branches of western white pine were reported by Lachmund (1934a) to have slightly thicker bark than trunks of a similar diameter.

The significant difference in total longitudinal growth rates found in this study between cankers for which the proportion distal was alive and those for which it was dead is at least partly explained by the nature of this study in which we are attempting to

reconstruct past canker expansion. Total canker expansion includes expansion in both longitudinal directions from canker center, but we have not estimated how long the branches/stems distal to the canker have been dead. Therefore, total canker expansion would include cankers which are no longer expanding distal to the canker center. As such, proximal canker expansion may be a more reliable measure of canker expansion. That those branches and stems that have the distal portion alive have significantly greater longitudinal growth rates despite having significantly smaller diameter branches/stems seems to indicate that the differences in longitudinal growth rates may not be related purely to the sampling method. The relationship between the condition of the branch or stem distal to the canker and proximal canker growth rates support this conclusion. This study found that there were significantly greater proximal canker growth rates in branches and stems with distal portions alive compared to those with distal portions dead. Buchanan (1938) also reported a slightly higher proximal growth rate on branches for which the portion distal to the canker was alive versus those for which it was dead, though the difference was not significant. Working in northern Idaho on WPBR infected western white pine, Slipp (1951) found that proximal canker growth was significantly higher on branches for which the portion distal to the canker was dead than for those with distal portions alive, but that the actual differences in growth rates amounted to approximately 0.4 cm/yr for the range of branch diameters most often encountered. As an obligate parasite, the pathogen serves as a sink for photosynthates and minerals transported in phloem. Presumably, cankers for which the portion distal is alive have a more immediate and larger source of these materials, which may explain, in part, the

greater canker growth rates associated in this study with cankers for which the portion distal is alive.

Proximal canker growth in limber pine averaged 4.9 cm/yr and ranged from 1.3 cm/yr for branches in the smallest diameter class (0.1 – 1.7 cm) to 6.3 cm/yr of branches and stems in the largest diameter class (>4.5 cm). These findings are similar to those reported in other white pine species. Slipp (1951) reported that proximal canker growth in western white pine increased with increasing branch diameter up to branch diameters of 2.0 cm beyond which he lacked data to draw inferences. The conclusion reached by Slipp (1951) was that branch diameter is the most valuable criterion for estimating proximal canker growth rate; although in his study branch diameter was able to explain only 12.3% of the variation on proximal growth rates. Buchanan (1938) analyzed proximal canker growth rates in western white pine in Idaho and found that annual proximal canker growth ranged from 3.2 cm/yr on small diameter branches to 6.3 cm/yr on larger diameter branches. Branch diameter explained 22.8% of the variance in proximal growth rates, and Buchanan concluded that other factors must be influencing proximal canker growth. The proximal canker growth rates in sugar pine reported by Harvey (1967) ranged from approximately 1.3 to 3.0 cm/yr. Harvey (1967) reported that proximal canker growth in sugar pine was 1.7 to 1.8 times less that found in western white pine by Buchanan and that proximal branch diameter explained only 2.5% of the variance in proximal growth rates. Phelps and Weber (1969) reported that proximal growth rate of branch cankers on eastern white pine ranged from 4.8 cm/yr for the smallest diameter class (0 – 1.3 cm) to 5.3 cm/yr for branches greater than 4.3 cm in diameter. Rhoads (1920) also found that

proximal canker growth exceeded distal canker growth in eastern white pine. Branch and stem diameters explained 6.6% of the variation on proximal canker growth rates found in this study. Other factors that may be affecting proximal growth rates in limber pine include genetics of both the host and the pathogen, water relations, and host anatomy (Lachmund 1934a). Lachmund (1934a) reported that canker growth slowed for a time at the nodes, especially when many nodes were present and those present were enlarged.

Circumferential growth rates of WPBR cankers on limber pine in this study averaged 6.5 cm/yr. Circumferential growth rates reported by Lachmund (1934a) ranged from 8.5 cm/yr on sites that were located in the zone considered optimal for western white pine growth to 6.4 cm/yr at high elevation sites. Circumferential growth rates averaged approximately 40% of the longitudinal growth rates (Lachmund 1934a). Rhoads (1920) found that circumferential growth rates, which overall averaged 6.4 cm/yr, were approximately 50% of those found for longitudinal growth rates in eastern white pine. In this study, circumferential growth rates could only be calculated for those stems and branches with portions distal to cankers having died as a result of branch girdling. For the limber pine cankers examined in this study, circumferential growth rates were approximately 88% of total longitudinal growth rates on girdled branches and stems. While the mean circumferential growth rate is similar to those reported in other species of white pines, it represents a much higher proportion of total longitudinal canker growth. This again relates to the earlier discussion on the limitation of total canker expansion rates on girdled branches and stems, which by definition includes cankers that are no longer expanding distal to the canker center.

The lack of a relationship between both total longitudinal and proximal canker growth rates and the sites from which cankers were collected suggests that the growth rates found in this study are applicable throughout the study areas. The lack of a relationship between elevation and canker growth rates was surprising. We had anticipated that limber pine growing at higher elevations would exhibit slower annual growth due to a shortened growing season. Hunt (1982), working in western white pine in British Columbia, found no correlation between canker growth rate and either elevation or biogeoclimatic zone. However, Lachmund (1934a) reported that regional site conditions were closely correlated with canker growth rates in western white pine. The cankers collected from sites at the highest elevations with the shortest growing seasons had lower growth rates than did those collected from sites near sea level on which conditions were considered optimal (Lachmund 1934a). Our failure to detect a similar relationship between elevation and longitudinal canker growth rate may be due in part to the relatively small elevation range from which cankers were collected in the study (2290 – 2895 m). It is also possible that trees at lower elevations experience more drought related stress that may result in slow canker growth rates at lower elevations. This is supported by the significantly greater canker growth rates found on plots located at the bases of slopes which are typically moister sites than those located along slope shoulders.

The canker growth rate models developed herein can only explain 44% of the variability in canker growth rates based on diameter of the stem or branch proximal to or below the canker, the condition of the branch or stem distal to the canker, and the branch height.

These models provide better prediction than those using proximal diameter alone, which could explain 9.5% of the variance in total longitudinal growth rates in this study and from 2.5 to 22.8% of the variance in proximal growth rates as reported by Buchanan (1938), Harvey (1967), Rhoads (1920), and Slipp (1951). The significant relationship between branch height and canker growth rate is a result of the significant interaction between condition distal to the canker and branch height. For branches with portions distal to the canker alive, the effect of branch height was significant. Typically branches higher in tree canopies are smaller in diameter and have correspondingly thinner bark. As this pathogen grows through and inhabits inner bark tissues, branches and stems with more inner bark tissues will promote growth of the fungus (Mielke 1943).

Our estimates of duration of infestation appear to be reasonable based on previous detection scouting reports. In general, the estimated period of infestation decreases to the south. Previous reports on the distribution of WPBR indicate that the pathogen first became established in the northwestern and north-central portions of Wyoming then spread to the south and east. In 1950, blister rust was observed for the first time infecting pine in Park County, Wyoming (USDA Forest Service 1951), which is located in the northwest portion of the state and includes portions of Yellowstone National Park. In 1966, the first WPBR infection in pine was reported at the northern edge of the Shoshone N.F. (Brown 1967). WPBR infection centers located along the east side of the Bighorn Mountains were first reported in a 1959 scouting report (USDA Forest Service 1959), but could not be confirmed until 1966. WPBR cankers were present in low numbers in 1982 at the Pole Mountain area of the Medicine Bow N.F. (B.W. Geils, personal

communication), and the first report in northern Colorado was in 1998 on the Roosevelt N.F. (Johnson and Jacobi 2000). Our sample of active cankers illustrates the same general expansion pattern, with the notable exception of the Horse Creek area of the Shoshone N.F. Explanations for this discrepancy are that the pathogen only recently became established or that infection episodes are relatively rare at this site, and while infections of pines may have been present in the 1960s, our sample of active cankers failed to capture older (bigger) cankers that have become inactive and deteriorated to the point of being unrecognizable. Infrequency of infection episodes would result in many cankers of the same length but few cankers in various size classes. The result of this may be that any cankers present in the 1960s were no longer available for sampling in our survey and conditions were not suitable for pine infections to occur again until the mid-1990s.

The objectives of this study were to determine the relationship between canker length and time since infection, and to create a canker growth rate model that would allow investigators to estimate the length of time that the pathogen has been infecting limber pines in an infested area and the number of infection episodes that have occurred. Results show a clear relationship between canker length and time since infection. Based on this relationship one can estimate both the period of infestation and the number of infection episodes that have occurred on a particular site, which should aid in reconstructing infection histories. However, this study was based solely on actively growing cankers, and as such cankers that have become inactive were not evaluated. Any reconstructions of infection histories must take this into account and recognize that

estimations of periods of infestation may be underestimated. Our attempts at developing a canker growth rate model reinforce those made by earlier researchers in other species of white pine. While there is a relationship between growth rate and branch or stem diameter, there is also a lot of variability that cannot be explained by the developed models. Studies in western North America are currently tracking annual canker growth rates in western white pine (J. Schwandt, pers. comm.) and limber pine (J. Blodgett, pers. comm.). These studies should provide greater insight into the causes of variability in canker growth rates and allow for the development of more accurate models. In the mean time, the models developed herein can be of use in the creation of models that assess risk to native limber pine populations over time.

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Figure 3.1. The spread and distribution of *Cronartium ribicola*, causal agent of white pine blister rust since its separate introductions to eastern and western North America.

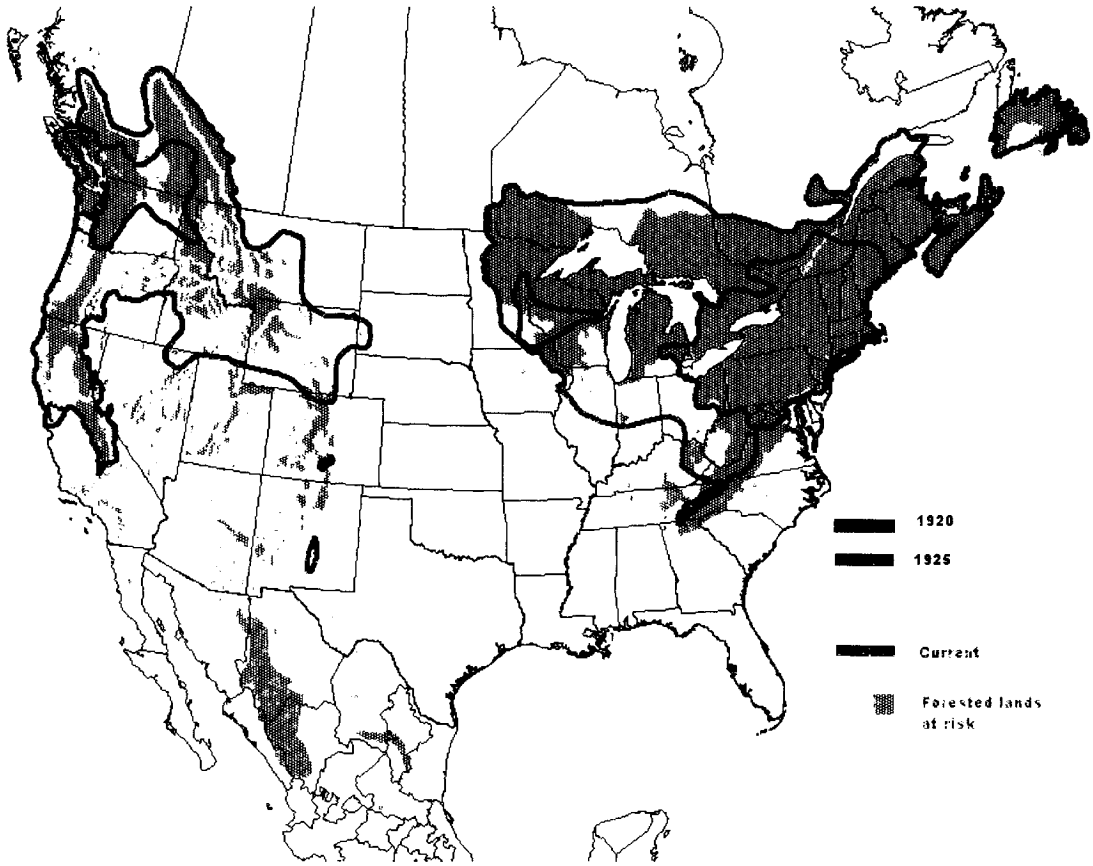


Image from Samman et al. 2003.

Figure 3.2. White pine blister rust canker length survey and canker collection areas in central and southeastern Wyoming and northern Colorado.

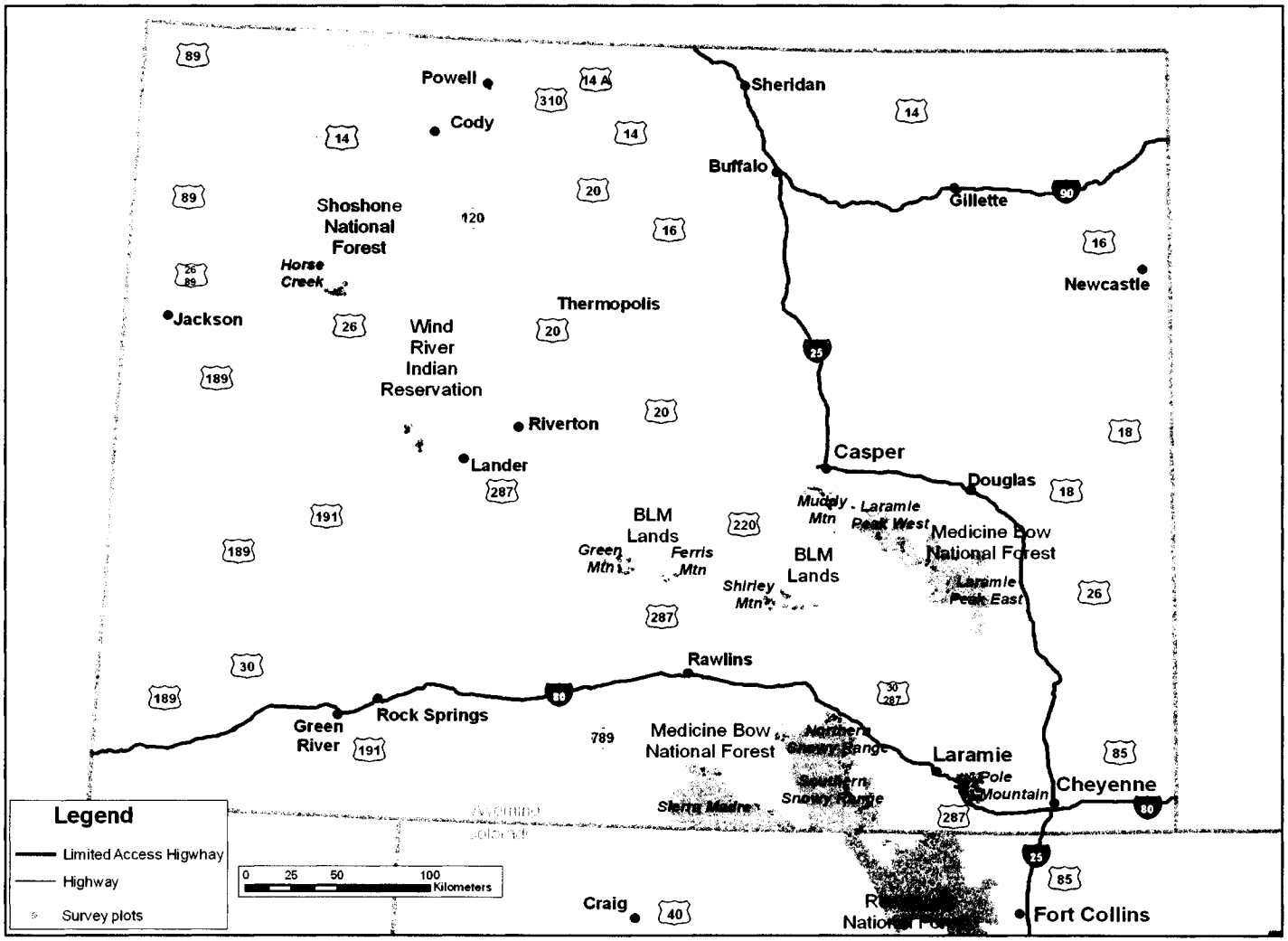


Figure 3.3. Cross section through a canker showing a) the entire canker disc and b) a close up of the area with two partial rings formed beyond the first cambial mortality and the orange stain which in this sample appears two years before the last complete ring.

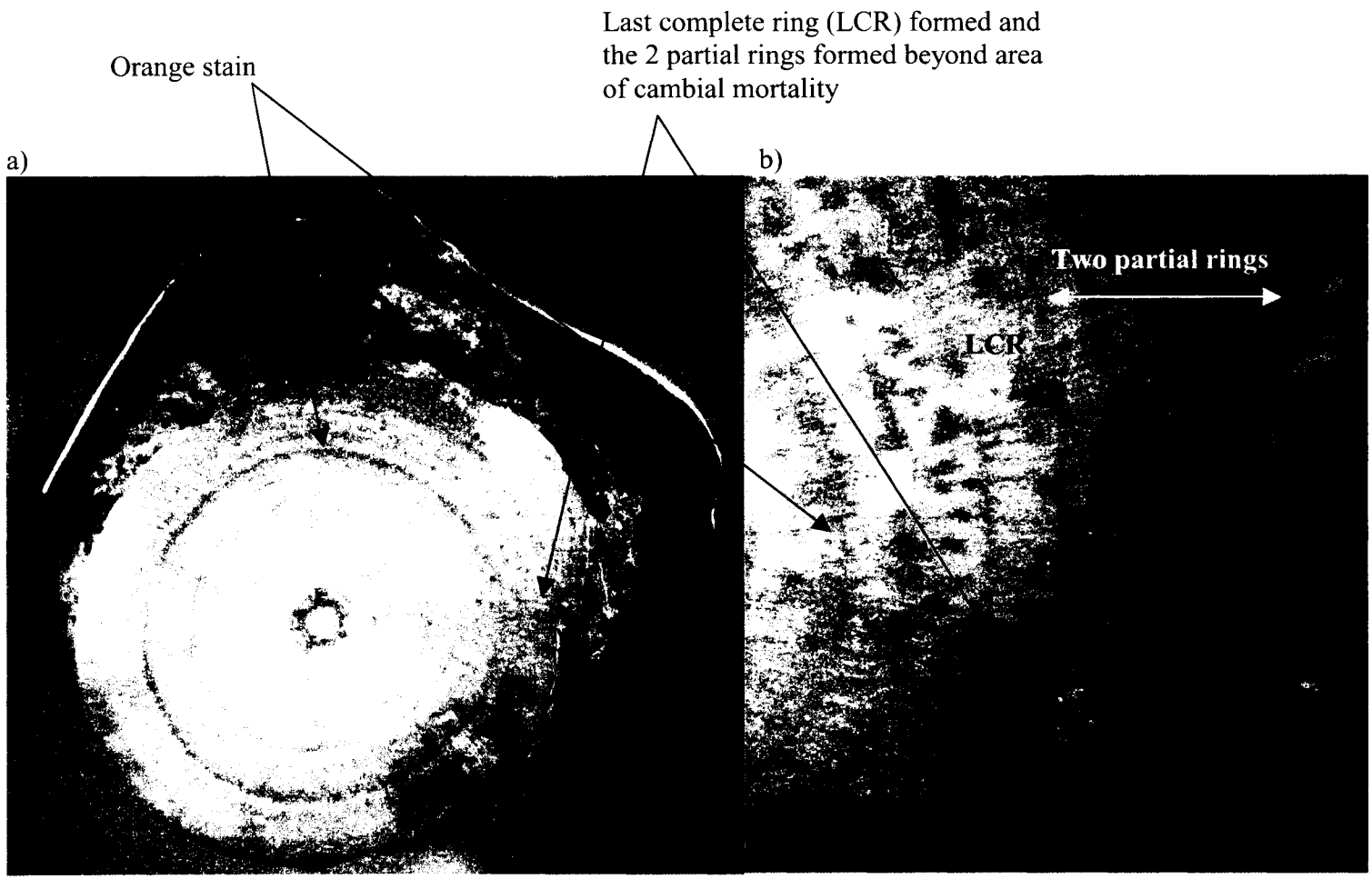
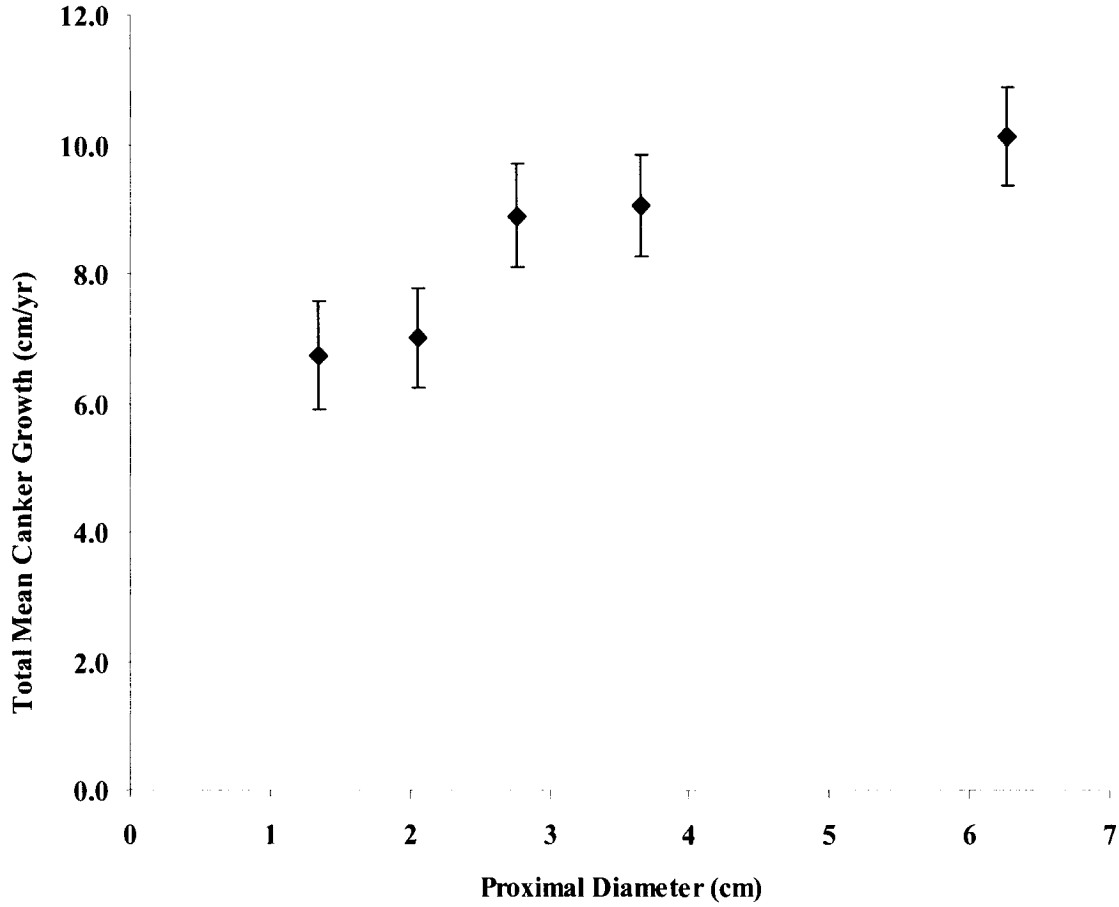
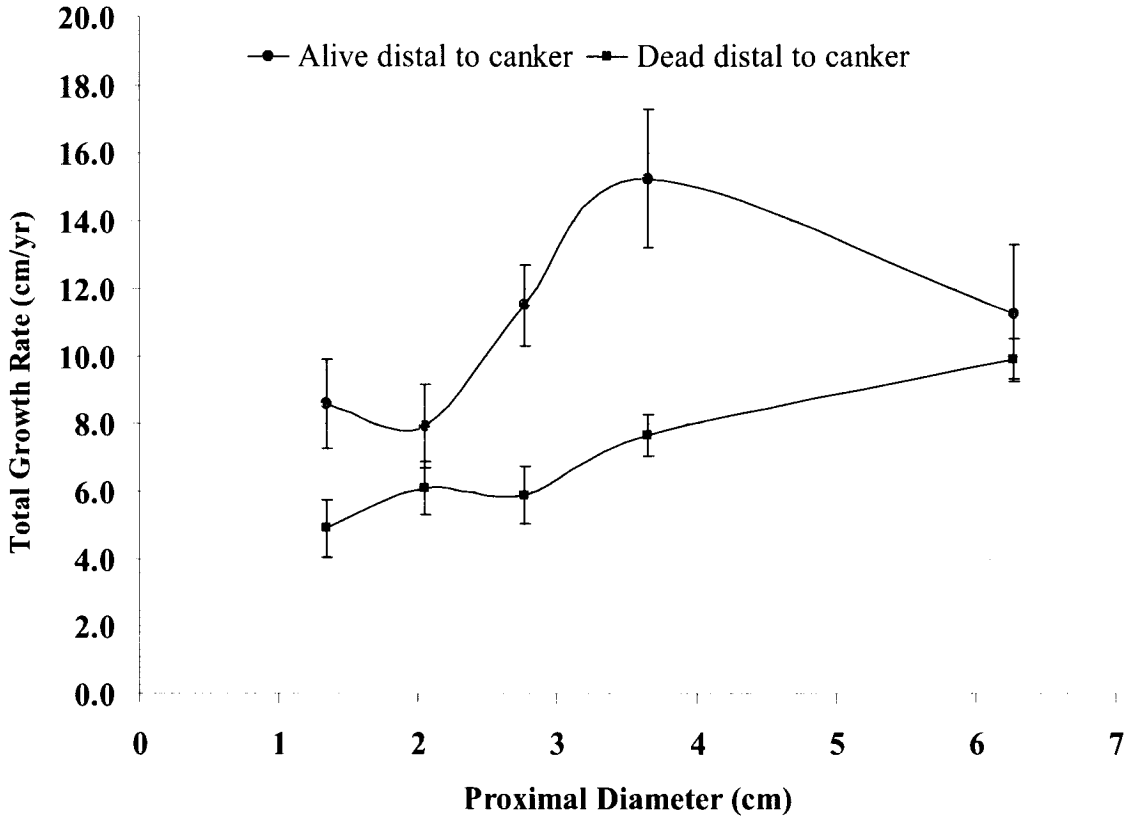


Figure 3.4. Relationship between total longitudinal canker growth rate and proximal branch/stem diameter. Points represent the midpoints of 5 diameter classes[1] and associated mean longitudinal canker growth rates.



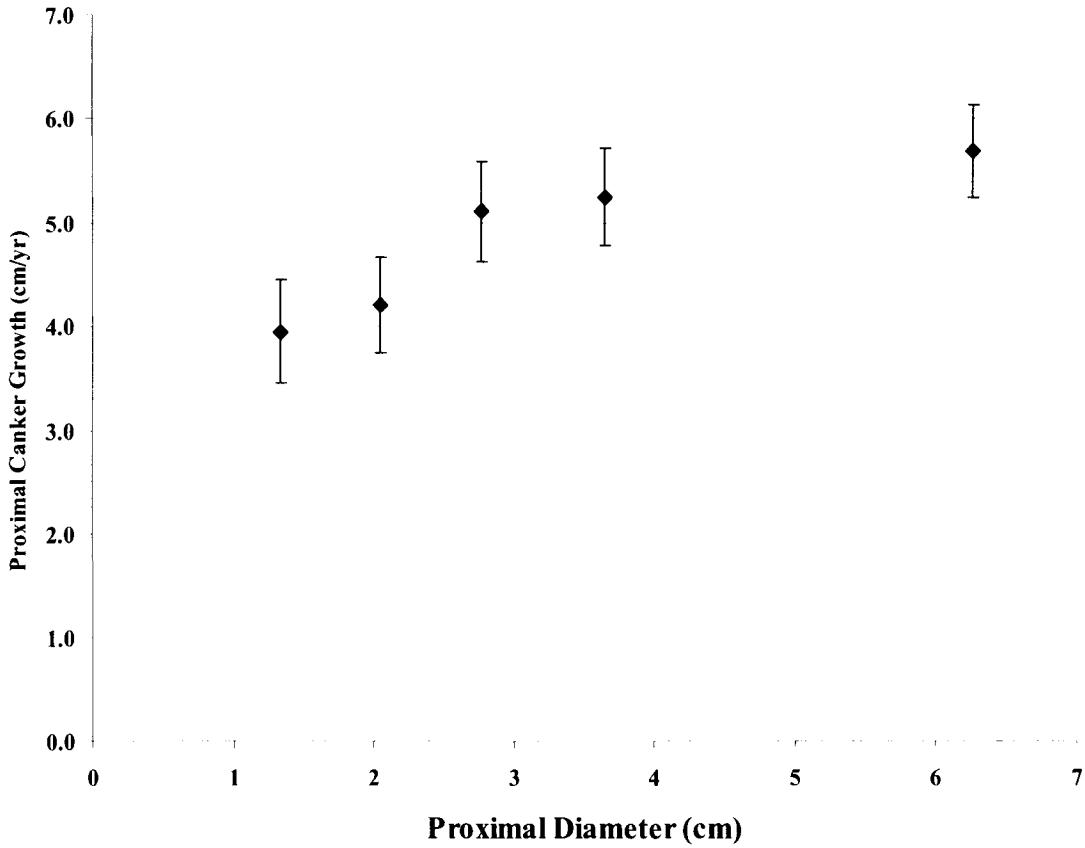
[1]Diameter classes: 0.1 - 1.7 cm (1.34 cm midpoint) n=24, 1.8 – 2.4 cm (2.05 cm midpoint) n=28, 2.5 – 3.1 cm (2.77 cm midpoint) n=26, 3.2-4.4 cm (3.65 cm midpoint) n=27, >4.5 cm (6.27 cm midpoint) n=29.

Figure 3.5. Relationship between total longitudinal canker growth rate and proximal branch/stem diameter, based on the condition of the portion of the stem/branch distal to the canker. Points represent the midpoints of 5 diameter classes[1] and associated mean longitudinal canker growth rates.



[1]Diameter classes: 0.1 - 1.7 cm (1.34 cm midpoint), n alive=12, n dead=12; 1.8 – 2.4 cm (2.05 cm midpoint), n alive=14, n dead=14; 2.5 – 3.1 cm (2.77 cm midpoint), n alive=14, n dead=12; 3.2-4.4 cm (3.65 cm midpoint), n alive=5, n dead=22; >4.5 cm (6.27 cm midpoint), n alive=5, n dead=24.

Figure 3.6. Proximal canker growth rate and proximal branch/stem diameter. Points represent the midpoints of 5 diameter classes[1] and associated mean proximal canker growth rates +/- 1 standard error.



[1]Diameter classes: 0.1 - 1.7 cm (1.34 cm midpoint) n=24, 1.8 – 2.4 cm (2.05 cm midpoint) n=28, 2.5 – 3.1 cm (2.77 cm midpoint) n=26, 3.2-4.4 cm (3.65 cm midpoint) n=27, >4.5 cm (6.27 cm midpoint) n=29.

Figure 3.7. Longitudinal growth rate model for branch cankers at mean branch height of 2.15 m.

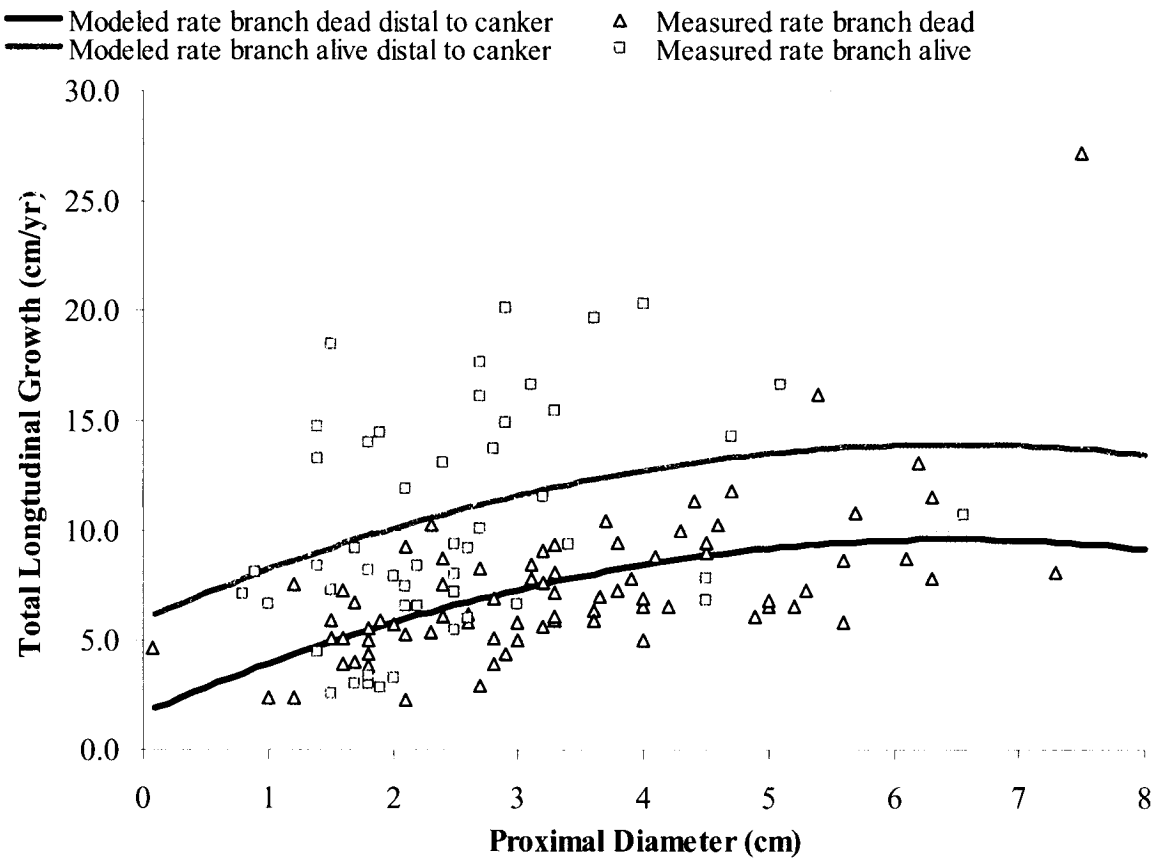


Table 3.1. Mean maximum canker lengths (cm) and standard errors by study site in central and southeastern Wyoming and northern Colorado.

		Maximum Canker Length		
Site	**N[1]**	**Mean (cm)**	**Tukey[2]**	**S. E.**
Laramie Peak West	11	91.9	a	11.7
Laramie Peak East	19	85.7	a	8.9
Wind River	15	68.1	ab	10.0
Northern Snowy	11	67.9	ab	11.7
Muddy Mountain	19	62.4	ab	8.9
Green Mountain	22	57.3	abc	8.2
Pole Mountain	85	56.0	abc	4.2
Shirley Mountains	28	50.6	abc	7.3
Ferris Mountain	4	45.7	abc	19.3
Horse Creek, SNF	19	20.5	bc	8.9
Roosevelt NF	20	19.6	bc	8.7
Southern Snowy	5	10.2	c	17.3
Total	258	54.4		2.6

[1] Number of plots on which canker lengths were recorded.

[2] Values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 3.2. Mean median canker lengths (cm) and standard errors by study site in central and southeastern Wyoming and northern Colorado.

		Median Canker Length		
Site	**N[1]**	**Mean (cm)**	**Tukey[2]**	**S. E.**
Laramie Peak West	11	74.6	a	4.9
Laramie Peak East	19	63.4	a	3.7
Northern Snowy	11	21.8	b	4.9
Pole Mountain	85	19.9	b	1.8
Muddy Mountain	19	16.5	b	3.7
Shirley Mountains	28	13.1	b	3.1
Ferris Mountain	4	12.4	b	8.1
Wind River	15	11.8	b	4.2
Roosevelt NF	20	9.9	b	3.6
Green Mountain	22	9.6	b	3.5
Horse Creek, SNF	19	8.5	b	3.7
Southern Snowy	5	6.1	b	7.3
Total	258	21.2		1.5

[1] Number of plots on which canker lengths were recorded.
[2] Values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Table 3.3. Correlation matrix for total canker lengths (cm) and white pine blister rust on 504 plots established in central and southeastern Wyoming and northern Colorado. All r-values (Pearson correlation coefficients) are significant at p<0.0001.

	Maximum Canker	**Median Canker**
Incidence[1]	0.642	0.309
Severity 1[2]	0.494	0.251
Severity 2[3]	0.471	0.410

[1] Percent limber pine infected by WPBR
[2] Number of cankers, both branch and stem, per infected limber pine
[3] Number of stem cankers per infected limber pine

Table 3.4. The range in time as of 2005 since initial infection at 13 white pine blister rust study sites in central and southwestern Wyoming and Colorado, arranged from north to south, based on maximum canker length recorded at each site and mean, maximum, and minimum canker growth rates.

Site	N[1]	Maximum canker[2] (cm)	Years mean rate[3]	Years max. rate[4]	Years min. rate[5]	Previous Survey Year	Previous Survey P/A[6]
Horse Creek, SNF	243	48.8	7.8	5.8	13.6	1969	A
Wind River	897	152.4	19.1	13.0	37.3	1969	A
Muddy Mountain	444	152.4	20.1	14.0	38.3	1969	A
Laramie Peak West	49	152.4	21.1	15.0	39.3	none	A
Green Mountain	220	213.4	28.4	19.8	53.8	1969	A
Laramie Peak East	100	121.9	17.5	12.6	32.0	1969	P[7]
Ferris Mountain	387	91.4	12.9	9.2	23.8	1969	A
Shirley Mountains	222	121.9	17.5	12.6	32.0	1969	A
Northern Snowy	50	182.9	24.8	17.4	46.5	1969	A
Pole Mountain	810	165.1	22.7	16.0	42.3	1982	P
Southern Snowy	34	15.2	4.8	4.2	6.6	none	A
Sierra Madre	0	0.0	0.0	0.0	0.0	none	A
Roosevelt NF	214	61.0	9.3	6.8	16.5	1998	P

[1] Number of canker lengths recorded at the site.
[2] Maximum canker length recorded within site.
[3] Number of years pathogen present based on mean canker growth rate (8.4 cm/yr).
[4] Number of years pathogen present based on maximum canker growth rate (12.7 cm/yr = mean growth rate + 1 SD).
[5] Number of years pathogen present based on minimum canker growth rate (4.2 cm/yr = mean growth rate – 1 SD).
[6] Reported presence (P) or absence (A) of white pine blister rust as of last survey year.
[7] WPBR reported in 1969 in area 16 km west of current survey plot locations.

Appendix 3.1. Relationship between total longitudinal canker growth rate, proximal branch/stem diameter, and the condition of the portion of the stem/branch distal to the canker for 134 white pine blister rust cankers collected from limber pine in central and southeastern Wyoming and northern Colorado.

Proximal Diameter (cm)	Class Midpoint (cm)	All Cankers N	All Cankers Mean Total Growth (cm/yr)[1]	All Cankers SE	Distal Portion Alive N	Distal Portion Alive Mean Total Growth (cm/yr)[1]	Distal Portion Alive SE	Distal Portion Dead N	Distal Portion Dead Mean Total Growth (cm/yr)[1]	Distal Portion Dead SE
0.1 - 1.7	1.34	24	6.73 a	0.84	12	8.58 a	1.32	12	4.88 a	0.84
1.8 - 2.4	2.05	28	7.01 a	0.77	14	7.92 a	1.22	14	6.10 a	0.78
2.5 - 3.1	2.77	26	8.90 ab	0.80	14	11.49 ab	1.22	12	5.88 a	0.84
3.2 - 4.4	3.65	27	9.07 ab	0.79	5	15.25 b	2.04	22	7.66 ab	0.62
> 4.5	6.27	29	10.13 b	0.76	5	11.27 ab	2.04	24	9.90 b	0.60
Total		134	8.42	0.37	50	10.15	0.57	84	7.39	0.44

[1]Values within columns followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Appendix 3.2. Relationship between proximal canker growth rate and proximal branch/stem diameter for 134 white pine blister rust cankers collected from limber pine in central and southeastern Wyoming and northern Colorado.

Diameter (cm)	Class Midpoint (cm)	N	Mean Proximal Growth (cm/yr)[1]		SE
0.1 - 1.7	1.34	24	3.95	a	0.50
1.8 - 2.4	2.05	28	4.21	a	0.46
2.5 - 3.1	2.77	26	5.11	a	0.48
3.2 - 4.4	3.65	27	5.25	a	0.47
> 4.5	6.27	29	5.69	a	0.45

[1]Values followed by different letters are significantly different at p=0.05 based on Tukey's HSD test.

Chapter 4.

Modeling white pine blister rust: the risk of establishment and potential damage to native white pine populations in Colorado and Wyoming

Introduction

Biological and physical aspects of ecosystems create spatial heterogeneity and contribute to the patchy distribution of forest pathogens (Nelson et al. 1999). Plant diseases occur when there is a compatible interaction between susceptible hosts, virulent pathogens, and conducive environments. Environmental factors determine disease severity and incidence in areas where both the pathogen and host are present, and climate is often the driving abiotic factor in determining disease incidence and severity (Weltzien 1988). Many pathogens have stringent climatological requirements for host infection. Weltzien (1988) indicated that if the relationships between the ecological and environmental factors controlling disease development and spread are well understood, the potential for disease to occur on a particular host at a particular location could be subject to forecasting. Risk and hazard rating models have been developed for many plant and forest diseases. Throughout this paper risk refers to the likelihood of pathogen establishment and hazard refers to the likelihood and amount of tree damage (Hunt 1983, Geils et al. 1999). Hazard can be described by incidence, the proportion of trees infected, and by severity, the amount of disease, or, in the case of white pine blister rust (WPBR), branch and stem cankers, per tree. Models have been created that utilize complex

meteorological data, tree growth and yield, disease biology and associated impacts, and economic and social values to examine and predict the spread, risk of attack, and the long and short-term effects of pest disturbances (Van Sickle 1992). Some of the risk and hazard models developed for forest pests include Douglas-fir tussock moth, spruce budworm, dwarf mistletoe, mountain pine beetle, spruce beetle (Van Sickle 1992), Armillaria root disease (Kallas et al. 2003, Byler et al. 1990), comandra blister rust (Jacobi et al. 1993), fusiform rust (Froelich and Snow 1986, Borders and Bailey 1986), stalactiform blister rust (Beard et al. 1983), sudden oak death (Meentemeyer et al. 2004), and laminated root rot (Williams and Marsden 1982, Byler et al. 1990) among others including white pine blister rust.

Epidemiology is the study of the temporal and spatial changes that occur in disease incidence, distribution, and control (Hawksworth et al. 1995). White pine blister rust epidemiology is strongly affected by genetics, profusion of inoculum, nearness and distribution of hosts, and microclimate (Geils et al. 1999). *Cronartium ribicola* (J.C. Fisch.), the pathogen that causes WPBR, has one of the most complex life cycles among the Fungi. Its life cycle involves five spore stages (macrocyclic) and two hosts (heteroecious) (Kendrick 2000). Each of the spore stages of this pathogen has specific environmental conditions necessary for production and germination, and some spore stages are more sensitive to temperature and moisture requirements than others (Van Arsdel et al. 1956). Factors that restrict and promote production of spores and infection of hosts must be known before predictions of likelihood of infection can be made (Peterson and Jewell 1968). Infections in the white pine host are perennial and result in

the formation of cankers. The first spore produced on the white pine host is the pycniospore, or spermatium, through which fertilization, or nuclear transfer, occurs. Pycniospores are released under warm temperature conditions in gelatinous droplets in the same area of the host that typically produces aeciospores in the next season (Lachmund 1933, Mielke 1943). Aeciospores are produced in early summer and then are dispersed to and infect *Ribes* hosts under suitable environmental conditions. Aeciospores can be dispersed on wind currents more than 500 km and potentially much further (Mielke 1943, Geils 2000, Van Arsdel et al. 1998). Production of aeciospores occurs at temperatures ranging from 16 to 28°C and requires exposure to saturated air (Van Arsdel et al. 1956). Germination of aeciospores occurs at temperatures from 8° to 24°C and requires free moisture or saturated air (Van Arsdel et al. 1956). Optimal germination of aeciospores has been reported at 20°C by McDonald et al. (1981) and at 16°C by Van Arsdel et al. (1956).

Urediniospores are produced on the *Ribes* host and act to increase the amount of infection in *Ribes* by producing more urediniospores capable of infecting *Ribes*. McDonald et al. (1981) examined the behavior of urediniospores and determined that due to their electrostatic behavior they were likely dispersed by insects and water rather than by wind, which would limit their dispersal to mainly within the same bush that was initially infected by an aeciospore. Urediniospores may also germinate directly to produce telia on which the next spore stage, the teliospore, is produced. Urediniospore production occurs at daytime temperatures ranging from 16 to 28°C and corresponding nighttime temperatures of 2 to 20°C, but they were never produced when daytime temperatures

reached 35°C (Van Arsdel et al. 1956). Optimal germination of urediniospores requires free water and occurs at 20°C, though germination does occur from 16 to 28°C (Van Arsdel et al. 1956). Whether a urediniospore produces uredia or telia depends largely on temperature; those kept at 21°C produced a combination of both uredinia and telia and while at 13°C urediniospores produced mainly telia (McDonald et al. 1981). Teliospores are produced by telia on the *Ribes* leaf and are not disseminated. They germinate in place to produce basidia, which in turn produce basidiospores. Fertile teliospores can be produced at temperatures ranging from 1 to 20°C, temperatures in excess of 24°C reduce their fertility, and teliospores were never produced when plants were exposed to daytime temperatures of 35°C (Van Arsdel et al. 1956). In general, teliospores will germinate when day and nighttime temperatures vary from 2 to 21°C, but the rate of germination depends on the temperature at which they were formed and the periodicity of wet periods (McDonald et al. 1981, Van Arsdel et al. 1956).

Basidiospores are the spores that are produced on the *Ribes* host that must disperse to a suitable white pine host and germinate for pine infection to occur. Krebill (1971) speculated that low temperatures at higher elevations prevented the production of basidiospores and limited the distribution of WPBR to sites below 2440 m elevation in the Rocky Mountains. In laboratory experiments he showed that basidiospores were produced at temperatures from 3 to 15°C, but that there were only a few hundred basidiospores cast at 3°C compared to several thousand cast at 15°C (Krebill 1971). Other researchers have suggested that while production of basidiospores occurs from 0 to 21°C, optimal basidiospore production occurs between 10 and 18°C (Hirt 1942). Free water or relative humidity of 97% or greater is necessary for basidiospore germination.

Free water in the form of rain was most important for pine infection and basidiospore production, followed by free moisture in the form of fog and then dew (Hirt 1942). Hirt (1942) showed that constant temperatures of 20-20.5°C and above prevented infection of the pine host. Pine host species may have an influence on these temperature effects, Bega (1960) found that germination of basidiospores on sugar pine (*Pinus lambertiana*) needles took place at temperatures that ranged from 0.5-1° to 28°C. Van Arsdel et al. (1956), working with eastern white pine, concluded that a 48 hour period in which the air remained saturated and temperatures did not exceed 20°C was required for the production and germination of basidiospores and the subsequent infection to the white pine host to occur.

WPBR models developed in other areas

McDonald et al. (1981) developed a complex computer simulation model with the goal of bringing together available information on WPBR to provide knowledge of WPBR epidemics under a series of conditions. The computer simulation model consists of a succession of submodels that compute *Ribes* density, the amount of *Ribes* infection, the size of the pine target available for infection by the rust, the number of pine infections that will occur per tree, and, finally, the incidence of WPBR within the stand of trees (McDonald et al. 1981). The simulation model is a notable attempt to consolidate and make sense of nearly a century of data collected by various scientists on WPBR. However, the model is also a hypothesis regarding the WPBR pathosystem and as such requires testing and calibration. One of the major benefits of the computer simulation model is that it allows one to examine the influence of individual variables. Through developing this model, McDonald et al. (1981) also characterized gaps in our current

knowledge, which can serve to direct future research. The model is currently being calibrated (J. Schwandt pers. comm.), and its utility in assisting in the formulation of management directives is unknown.

For managed western white pine stands in northern Idaho, eastern Washington, and western Montana, a preliminary expert hazard rating system was developed based on habitat type and potential *Ribes* density based on site preparation method, slope aspect, and the amount of disturbance to the duff layer (Rust 1988). A rust index, or current rust hazard, measured as the number of cankers per thousand needles per year accumulated over a minimum of ten years, was recommended by Hagle et al. (1989) as the best basis for determining future hazard for the regeneration of western white pine stands in Northern Idaho and Western Montana. Rust hazard could also be estimated by measuring within stand *Ribes* populations, but this method was not considered as effective as the rust index (Hagle et al. 1989). Hunt (1983) used slope percent, canker growth rate and mortality, and stem density to rate the hazard to white pines in British Columbia. Trees at the greatest hazard for damage were those that were open grown on slopes, while those growing in dense stands in flat areas had the lowest hazard. Proximity to *Ribes*, microsite effects, and canker growth and mortality rates resulted in slight variations in hazard (Hunt 1983). Geils et al. (1999) developed a preliminary hazard model for southwestern white pine in New Mexico that was based on elevation, plant association, and topographic position. Smith and Hoffman (2001) created a series of logistic regression models to predict incidence of WPBR in southern Idaho and western Wyoming. Higher incidence was related to greater average stem diameter, lower elevation, greater mean summer

precipitation, the presence of *Ribes* species within the stand, lower stand densities, gentle slopes, topographic position, and habitat type.

Several white pine blister rust risk and hazard models have been developed in eastern North America. Charlton (1963) defined suitability of climate by mean monthly minimum temperature representing nighttime temperatures, mean monthly maximum temperature representing daytime temperatures, the average amount of rainfall in July and August and the frequency of rain events, and air movement to calculate the relative probability of weather conducive to pine infection. Temperature inversions, in which air temperatures at ground level are lower than those above, were considered favorable to infection, while air movements that promoted warm, dry conditions were considered unfavorable (Charlton 1963). Variables that Charlton used to evaluate air movement patterns at specific sites included altitude, land form, relief and soils, aspect and slope position, and vegetation cover. The ratings for each of the four factors were then multiplied to determine the overall probability of favorable weather for 14 eastern states from Virginia to Maine and west to Pennsylvania based on data collected from 928 weather stations. A map defining high, medium, and low hazard zones was then constructed and when compared to observed levels of WPBR seem to be generally well correlated (Charlton 1963). Gross (1985) presents a similar model for Ontario based on mean minimum and daily July temperatures, mean annual frost free period, mean date of first frost, and physiographic characteristics. Within the broad hazard zones identified through the model, microclimatic differences influenced infection hazard (Gross 1985). Lavallée (1986a and 1986b) defined hazard zones in Quebec based on elevation and

mean July and August temperatures. Once again the broadly defined zones correlated well with general level of WPBR infection, with microclimatic conditions within zones influencing incidence of infection (Lavallée 1986a, 1986b).

In modeling WPBR hazard in the Great Lakes States, Van Arsdel (1972) concluded that the distribution of WPBR was related to meteorological conditions at three scales. The highest order, or macro-scale, was controlled by latitude and general elevation; the intermediate, or meso-scale, was influenced by the specific elevations of hills and river valleys within an area, and the finest level, or micro-scale, was affected by stand structure and slopes within stands (Van Arsdel 1972). WPBR incidence in eastern white pine in Michigan, Wisconsin, and Minnesota was generally greater at more northern latitudes and higher elevations. Within the broadly delineated hazard zones, incidence was greater at the bases of slopes, in narrow valleys, and small forest openings, all of which tend to be cooler, moister sites (Van Arsdel 1972). Using these variables, they were able to predict the occurrence, or risk, of WPBR on a given site in southwestern Wisconsin with 89% accuracy (Van Arsdel 1972).

The circumstances leading to infection of white pines in other regions of North America may differ significantly from those occurring in the more arid central Rocky Mountains. Van Arsdel (1961) reported that in the Lakes States, 99% of WPBR cankers are located within 2m of the ground. Gross (1985) presents data from published reports from Ontario, in which 84% of cankers were less than 2m above ground level. In British Columbia, Hunt (1982, 1983) reported that while most of the cankers were close to the

ground (below 1.25m), WPBR cankers were found higher in the crown on steeper slopes. These reports indicate that moisture and temperature effects in proximity to the ground may be most important in determining risk and hazard of WPBR. In the central Rocky Mountain region, WPBR cankers are well distributed throughout tree crowns and are not limited to lower crown branches (Kearns unpublished data). Since host species; pathogen genetics (Hamelin et al. 2000, McDonald 2000); macrosite, microsite, and meteorological conditions; and disease occurrence are apparently different in the central Rocky Mountains, previous models developed to predict WPBR risk and hazard may not be applicable in this region. Thus, the objectives of this study were to develop models to predict the likelihood of *C. ribicola* establishment in Colorado's native white pine populations (risk) and to predict future incidence and severity of WPBR (hazard) based on site and meteorological variables that will allow land managers to prioritize monitoring and, if necessary, control efforts in areas of high risk and hazard.

Methods

Survey

White pine blister rust surveys were conducted (Kearns 2005, Chapter 1) in 13 study areas located in central and southeastern Wyoming and northern Colorado (Figure 4.1) from 2002 - 2004. Data were collected in central and southeastern Wyoming and northern Colorado because the pathogen has been reported in various areas of Wyoming starting in the mid-1940s (USDA Forest Service 1950, Brown 1967) and more recently in northern Colorado in 1998 (Johnson and Jacobi 2000). At the initiation of this study, the pathogen was not known to be established elsewhere in Colorado outside of the

Roosevelt National Forest in northern Colorado. In 2003, isolated WPBR infestations were discovered in the Wet and Sangre de Cristo Mountains of southern Colorado, more than 450 km from other known infections. Limber pines (*Pinus flexilis* James) were infected in these new areas, and the first known natural infections on Rocky Mountain bristlecone pine (*P. aristata* Engelm.) were also discovered (Blodgett and Sullivan 2004). The data collected on the 504 plots established during these surveys included tree-level information on number of branch and stem cankers, diameter class, crown class, percent live crown, and health status. Plot-level data collected included GPS coordinates, elevation, slope percent, aspect, slope position, slope configuration, stand structure, and dominant tree and understory cover. In addition, data were collected on the presence and density of *Ribes* by species on the 504 WPBR survey plots and 754 extensive *Ribes* survey plots (Kearns 2005, Chapter 2).

Model Building

Preliminary Model

A preliminary model of hazard of WPBR infection was developed based on other models reported for white pines in the Rocky Mountains (Geils et al. 1999, Smith and Hoffman 2001). We based our preliminary model on five plot-level variables commonly available in the Rocky Mountain Resource Inventory System (RMRIS) database, a stand inventory database utilized by the USDA Forest Service in this region. The five variables employed and the relative hazard values assigned to each were as follows:

- Elevation: <2,590m - high hazard, 2,590-3,050m - moderate hazard, and >3,050m - low hazard.

- Aspect: N, NW, NE aspects – high hazard; E, W aspects - moderate hazard; S, SE, SW aspects – low hazard.
- Slope Percent: 0-15% - high hazard, 16-50% - moderate hazard, >50% - low hazard.
- Topographic Position: valley bottoms, toe and foot slopes – high hazard; mid slope – moderate hazard; ridges and slope shoulders – low hazard.
- Cover Type: Aspen, spruce/fir – high hazard; Douglas-fir/mixed conifer, limber pine, lodgepole pine – moderate hazard; rock, ponderosa pine – low hazard.

The relative hazard categories assigned to elevation were based on Smith and Hoffman (2001) reporting that 97% of plots established below 2591m were infested with WPBR compared to 53% above 2591. The relative hazard rating categories assigned for aspect, topographic position, cover type, and slope were based on moisture requirements for fungal spore germination and the assumed moisture holding capabilities of the various aspect, topographic classes, cover types, and the assumption that milder slopes retain more moisture (Charlton 1963, Gross 1985). The preliminary model was then used to assign a hazard rating for each of the 504 survey plots established. For each category, a 0, 1, or 2 was assigned for increasing hazard (Geils et al. 1999). The five relative hazard values were then summed for each plot giving a total hazard value that ranged from 0 to 10. Total hazard values exceeding 7 were assigned to the high hazard category, those with total hazard values of less than 5 were low hazard, and those with values of 5 or 6 were moderate hazard. Correlations and analysis of variance (ANOVA) were then preformed to evaluate the assigned hazard category with actual level of WPBR found at

each plot. Logistic regressions were run to determine the ability of the preliminary model to predict risk of WPBR. Statistical analyses were performed utilizing the SAS (version 9.1, SAS Institute Inc.) statistical program.

Risk of WPBR

Logistic Regression Model

The logistic procedure in SAS was used to develop a logistic regression model to predict the probability of WPBR at a given site. Data collected on 329 survey plots were used to develop the model. Survey plots located in the Sierra Madre, Southern Snowy Range, and Roosevelt National Forest areas were excluded from the model building effort due to either the complete absence of the pathogen (Sierra Madre) or the relatively recent establishment of the pathogen (Southern Snowy Range and Roosevelt National Forest). In these areas, WPBR was absent on the majority of plots established and thus, the pathogen has likely not yet been fully distributed or established in all suitable sites. Elevation, although significantly negatively correlated to incidence of WPBR (Kearns 2005, Chapter 1), was not allowed as a variable in any of the developed models. Our goal was to predict the presence of WPBR in Colorado's native white pines, but our survey data was obtained primarily in Wyoming due to the lack of known occurrence in Colorado. The effect of elevation on plant communities and likely associated pathogens changes with latitude. The distribution of Colorado's white pines at more southerly latitudes precludes the use of elevation data collected in more northerly latitudes in model building efforts.

In addition to the data collected through the WPBR and extensive *Ribes* surveys (Kearns 2005, Chapters 1 and 2), data from geographical information systems (GIS) on stream distribution and climate data were assembled. Climate data was obtained from PRISM, (parameter-elevation regressions on independent slopes model (Daly et al. 2002)) and included 30-year (1961-1990) monthly averages for minimum and maximum temperatures, precipitation, relative humidity, and median length of the frost free period. PRISM is a regression-based model that employs weather station data, digital elevation models, other spatial data, and expert knowledge and parameterization to develop reproducible estimates of annual and monthly climate components that are interpolated to a GIS grid (Daly et al. 2002). Due to the high correlation between temperature variables (i.e. plots with high mean August maximum temperatures also had high July and September maximum temperatures, Appendix 4.1), monthly temperature minimums and maximums were averaged for May and June, and July, August, and September. We divided the growing season into these two periods to correspond with the different periods of spore development in the *C. ribicola* life cycle that we observed in infested areas in Wyoming and Colorado. The May-June period is when production and germination of aeciospores and the subsequent infection of the *Ribes* host occurs. The July-August-September period captures the production and germination of teliospores and basidiospores. Urediniospores are produced and re-infecting *Ribes* in both time periods.

GIS layers on stream distributions were obtained from the National Forest Service (1:24000) and from the United States Geological Survey's National Hydrography Dataset (1:100000). Distance to nearest stream was determined by using the ArcInfo "Near" command which computes the distance from each point in a coverage to the nearest arc in another coverage. Stream density within a 1 km radius of the plot was calculated by generating a 1 km continuous density grid from the stream layer using the "Density" function within ArcMap/Spatial Analyst and then identifying the grid cell each plot fell within. Stream density values were multiplied by 1,000 for modeling purposes to reduce the number of digits beyond the decimal and to provide stream densities in kilometers of stream per square kilometer . Data collected from the extensive *Ribes* survey were incorporated by calculating the mean densities of *Ribes* by species for all extensive *Ribes* plots that fell in a 1 km radius of the WPBR survey plot.

Final model selection was based on the model that minimized the Akaike Information Criterion (AIC), maximized the Kappa statistic, and made biological sense from published accounts of the pathogen's life cycle. AIC provides a measure of the fit of the model, estimated error variance, against the model's complexity, where there is a cost for adding to the number of parameters (P. Chapman, pers. comm.). When attempting to assess the effectiveness of a predictor variable in correctly classifying observations, measuring the improvement over chance agreement is necessary (Fielding and Bell 1997). The Kappa statistic (K) provides a measure of prediction accuracy while incorporating a correction for chance-expected agreement (Fleiss 1981, Fielding and Bell 1997). Kappa statistic values <0.4 indicate poor agreement, $0.4<K<0.75$ indicate good

agreement, and K>0.75 indicate excellent agreement (Fielding and Bell 1997). The area under the receiver operating characteristic (ROC) curve is another measure of overall model accuracy (Fielding and Bell 1997). Values for areas under the ROC curve (AUC) range from 0.5 to 1.0, and indicate the proportion of time that a random observation in the positive category will have a greater score than a random observation from the negative category (Fielding and Bell 1997).

Data collected on 139 supplemental survey plots in four general areas (Roosevelt N.F., San Isabel N.F., Sangre de Cristo Mountains, and Wet Mountains) in Colorado that were positive for the presence of WPBR (Figure 4.2) were used to test the model's predictive ability. The supplemental surveys were performed by Colorado State University and USDA Forest Service crews using methods similar to the original survey. In addition, survey data collected on the Roosevelt National Forest and Southern Snowy Range study areas that were not used to develop the model, were used to evaluate the developed model. In all, data from 612 survey plots were used to evaluate models: 329 plots used to develop the model plus 283 survey and supplemental survey plots.

Classification and Regression Trees (CART)

We used the S-PLUS (version 7.0, Insightful Corp.) statistical program to develop classification and regression trees to model relationships between environmental and site variables and the presence/absence, or risk, of WPBR. Classification trees employ the multinomial statistical model in which splits are based on minimizing the deviance, which is defined by the multinomial log-likelihood (De'Ath and Fabricius 2000). This

approach is non-parametric and can employ categorical and continuous dependent and predictor variables. Classification trees to predict the presence/absence, or risk, of WPBR on a plot were constructed on plot variables alone and on the climate and plot variables together (Appendix 4.2). S-PLUS constructed the trees and determined the deviance associated with the ten-fold cross-validation in an attempt to select a tree that minimized the prediction error. Trees were then pruned to the reduced number of nodes that minimized deviance. Again, the survey plot data were restricted to those areas where the pathogen was present on the majority of established plots and consisted of the same 329 survey plots that were used to build the logistic regression model.

Mapping Modeled Risk

A base map used to identify white pine distributions in Colorado was developed from the following source layers: the Colorado Vegetation Classification Project, which is an unsupervised classification from 1993-1997 Landsat Thematic Mapper developed by Colorado Division of Wildlife and BLM; the Southwest Regional Gap Analysis Project, which is a seamless landcover of five-state region of southwestern US developed by consortium of institutions headed by the USGS; and Forest Inventory and Analysis, which is a USDA Forest Service developed inventory of average tree size and percent cover of tree stands using aerial imagery and field plots. In addition, data from the Rocky Mountain Resource Inventory System (RMRIS) database on the geographic location of stands containing limber pine were obtained for the Roosevelt National Forest. Data for white pine stands (limber pine, bristlecone pine, and southwestern white pine) were selected from each of these layers using codes obtained from their metadata. These four

white pine layers were then merged into one layer using ESRI's ArcToolBox with the Append function. For more efficient joining on the PRISM climate layers, a centroid point layer of these polygons was obtained using an ESRI ArcMap script. PRISM temperature, precipitation, and relative humidity data were then joined to the white pine points within ArcMap to obtain climate values for each center point of the white pine polygons. A stream density layer was developed within Arcmap Spatial Analyst using the Density function from a 100k Colorado stream layer from USGS's National Hydrography Dataset. This density layer was then joined with the white pine polygons within ArcMap to obtain average stream density within each polygon. Joining with centroid points was not used because the stream density layer was very fine and highly variable requiring averaging within polygons. The result of these GIS analyses was a layer of white pine polygons with attributes for all the climate and stream density values needed for the model calculations.

To develop the risk map based on the logistic regression model, calculations were performed within MS Excel and each polygon was labeled with the probability values. Classified risk maps were then produced showing color coded polygons indicating risk of WPBR. To develop the risk map based on the CART model, queries were developed within ArcMap for each branch of the classification tree. The white pine polygons were then labeled with either model predicted presence (1) or absence (0) values. Total surface areas for risk categories were obtained by first determining the highest model value for all overlapping white pine polygons and then merging these overlapping polygons within ArcMap. Merged polygons were labeled with this highest value. Using

ArcMap's Summarize function, a table of total polygon areas by probability ranges (based on the logistic regression model) and presence/absence (based on CART model) were then obtained.

Disease Pressure

Disease pressure is a measure of how often infection events occur on a given site. It is difficult to estimate when favorable climatic conditions exist for each of the spore stages in the life cycle of *C. ribicola* such that pine infection occurs. For example, if conditions are suitable in May and June for prolific production, germination, and infection of aeciospores, but conditions in August and September are either too hot or too dry to allow production, germination, and infection by basidiospores, no pine infections will occur on that site that year. On the other hand, conditions may be perfect for the basidiospore stage, but conditions in May and June were too cold or too dry to allow the initial infection of the *Ribes* plant and again no pine infections will occur on that site in that year. Essentially, any one period of unsuitable climatic conditions occurring during the growing season will significantly reduce the number of pine infections that occur (Mielke 1943). The times when optimal conditions coincide with spore production, dissemination, germination, and infection results in the sporadic spread and establishment of WPBR: the so-called "wave years" in which heavy pine infections occur (Mielke 1943). In predicting the amount of disease that will be present on site in future years, some knowledge of the disease pressure, or the number of times conditions are suitable for spread and pine infection to occur, is necessary.

Canker lengths were recorded on 258 of the WPBR survey plots. White pine blister rust cankers in limber pine had an average growth rate of 8.4 cm/yr (standard deviation 4.2 cm/yr) (Kearns 2005, Chapter 3). All recorded canker lengths were sorted into 15.24 cm canker size classes, or canker bins, a bin width that should capture the observed variability in canker growth rates. The number of canker bins occupied for each plot was then calculated. We used canker bins, or the number of canker size classes present at each plot, as a measure of disease pressure. For example, a plot with 4 recorded canker lengths of 5, 10, 12, and 32 cm would have 2 canker bins occupied, the 0.01-15.24 cm bin and the 30.5-45.7 cm canker bin. Multiple linear regression with stepwise selection was then used to model the number of canker bins occupied using meteorological and plot variables as the predictive variables. Final multiple regression model selection attempted to minimize Akaike Information Criterion (AIC), Mallow's Cp, and the predicted residual sum of squares (PRESS), while maximizing variance explained by the model (R^2). Model selection using the minimum Mallow's Cp statistic criterion, where the value of Cp is close to the number of parameters in the model, provides the model with the smallest mean squared prediction errors (Ott and Longnecker 2001, P. Chapman pers. comm.). The minimum PRESS statistic criterion minimizes the prediction error sum of squares and is recommended when the objective of the model is prediction (Ott and Longnecker 2001, P. Chapman pers. comm.). CART analysis was also used to examine important variables in determining the number of canker bins occupied on a given plot. Data collected on the 468 survey plots, all plots except those at Sierra Madre and five plots with missing variables, and their associated GIS variables were used to develop the models.

White Pine Blister Rust Hazard

We used both multiple regression and CART analyses to model WPBR hazard defined in terms of incidence. Incidence was defined as the number of infected trees/number of evaluated trees. Multiple linear regression with stepwise selection was used to model WPBR incidence as described above. Both a regression tree to model level of incidence and a classification tree based on categorical level of incidence, where category 1 = incidence <0.25, category 2 = 0.25 ≤incidence≥0.50, and category 3= incidence>0.50 were grown as described above. CART analyses were also used to model WPBR hazard in terms of severity, a measure of the amount of disease present per tree, which was calculated as a rust severity index (RSI) after Duriscoe and Duriscoe (2002). The RSI provides a relative measure of expected biological impact based on affected tree size and number and location of cankers (Appendix 4.3). To create the models we employed the data from 468 survey plots located in all study sites except the Sierra Madre, where no WPBR was found, and their associated PRISM and GIS variables.

Results

Preliminary Model

According to the preliminary model, 27% of the 504 plots surveyed were classified as high hazard, 46% were classified as moderate hazard, and 27% were classified as low hazard. Total hazard, the sum of the hazard values for each of the five criteria (elevation, aspect, slope percent, topographic position, and cover type), was weakly correlated with incidence ($r=0.226$, $p<0.001$). The total hazard value only explained 5.1% of the

variation in actual incidence ($F=27.04$, $p<0.0001$, $R^2=0.0511$). There were significant differences in mean incidence between the hazard categories. The high hazard category plots had a mean incidence of 23.2%, which was significantly higher than the mean 14.2% incidence of the moderate hazard category plots and the mean 10.0% incidence of the plots categorized as low hazard. The differences in mean incidence between the moderate and low hazard categories were not significant based on Tukey's honest significant difference (HSD) at $\alpha=0.05$. When hazard category was used as the predictor variable in logistic regression to predict the presence or absence of WPBR (or risk), prediction accuracy was 62.5% (K = 0.21, present=82%, absent=38.5%), indicating poor agreement between the hazard category and the presence of WPBR. When the total hazard value was used as the independent variable accuracy was 50.8% (K= -0.001, present=60.8%, absent=38.5%). Of the 278 plots that did have WPBR infected limber pine, 105 (37.8%) were classified as high hazard, 123 (44.2%) as moderate hazard, and 50 (18.0%) as low hazard. For the 226 plots that were not infested with WPBR, 30 (13.3%) were classified as high hazard, 109 (48.2%) were in the moderate hazard category, and 87 (38.5%) were classified as low hazard. Of the 137 low hazard plots, 36.5% had trees infected with WPBR; while on the 135 high hazard plots, 22.2% did not contain infected limber pine. These results indicate that the preliminary model developed herein does not provide an accurate estimate of WPBR risk in the central Rocky Mountains.

Risk of White Pine Blister Rust

Logistic Regression

The selected logistic regression model employed five variables to predict the risk of WPBR establishment. The results and parameter estimates for are shown in Table 4.1. The probability modeled was WPBR present. The model indicated that the probability of WPBR on a given plot increases with higher levels of both May and September relative humidity, higher average July-August-September maximum temperatures, and higher stream density within 1 km radius of the plot. The probability of WPBR decreases with higher average May-June maximum temperatures. The prediction accuracy of this model was 88.4% (K=0.653, present=95.3%, absent=65.8%), indication good agreement between actual and predicted presence of WPBR. The ROC curve for the logistic regression function is shown in Figure 4.3 and had an estimated area under the curve of 0.899 indicating that in approximately 90% of cases, a random observation in the WPBR present category will have a greater probability score than a random observation from the WPBR absent category.

In all, 16 study sites (10 study sites used to build the model and 6 new study sites) containing 612 survey plots were used to evaluate the model. A t-test showed that modeled risk, or predicted probability of WPBR, was significantly higher ($p<0.0001$) on plots that currently have WPBR (n=312) than at plots that are currently uninfested (n=300). The modeled estimated probabilities were averaged for each of the 16 study sites. Mean predicted probability within a given study area should be related to the proportion of infested plots to surveyed plots in that study area. The correlation between

mean predicted probability and observed percent of plots infested was positive ($r=0.874$, $p<0.0001$) for the 16 study areas (Table 4.2). From the graph depicting the relationship between mean predicted probability and observed proportion of infested plots (Figure 4.4), it is clear that the test plots located in the Sangre de Cristo Mountain Range have a much higher proportion of infested plots than the model indicates. For the remaining test plots in Colorado and the Southern Snowy Range the model predicts a higher occurrence of WPBR than is currently observed, suggesting that there may be an intensification of the disease in those areas with time as the pathogen expands its current distribution. The mean estimated probability based on the logistic regression model for the Sierra Madre plots at 0.475 indicates that the study site is not constitutionally inhospitable to the pathogen based on the model parameters even though our survey failed to locate any infected trees at that site.

The risk map developed from the logistic regression model is shown in Figure 4.5. According to the logistic regression model approximately 145,000 ha of white pine stands have a predicted probability of *Cronartium ribicola* being present greater than 0.50. This amount represents approximately 12% of the area containing white pines in Colorado based on the white pine distribution layer developed. The majority of the areas at risk according to this model are located along Colorado's Front Range. A close-up of the Roosevelt N.F. showing the predicted probability of the presence of *C. ribicola* is shown in Figure 4.6, which also displays the locations of survey plots and their associated presence or absence of WPBR.

CART

Classification trees for predicting the presence/absence, or risk, of WPBR were created. The classification tree based on plot variables contained 5 terminal nodes and included *Ribes inerme* density within 1 km radius of the plot, stream density within 1km radius of the plot, and the presence/absence of ponderosa pine as predictor variables (Figure 4.7). The Kappa statistic for this classification tree was 0.800, presence was accurately predicted 96%, absence was correctly predicted 83%, and total misclassification rate was 19.7%. The model suggests that probability of white pine blister rust is related to densities of *Ribes inerme* within a 1 km radius of the plot in excess of 607.6 m/ha, for the 120 plots that fell into this category the probability of WPBR was 0.942. When *R. inerme* densities were less than 607.6m/ha, the next splitting point that produces high probability of presence of WPBR is stream densities within 1 km of the plot in excess of 2.03 km of stream/km^2 land area. Then, when stream densities within 1 km of the plot were less than 2.03km/km^2 the next splitting point that produces a high probability of the presence of WPBR was the presence of ponderosa pine as one of the three dominant tree species on the plot. When ponderosa pine was absent, the classification becomes much weaker with 0.833 probability of the absence of WPBR at *R. inerme* densities greater than 106.4 m/ha and 0.580 probability of WPBR being present with lower *R. inerme* densities. This model could not be tested on the supplemental survey plots in Colorado, due to lack of information on *R. inerme* densities.

When all variables, including PRISM and plot variables, were entered as potential predictors of the presence of WPBR, only PRISM variables were selected. The

classification tree had 5 terminal nodes, with splits based on May relative humidity, May precipitation, May minimum temperature and August minimum temperature (Figure 4.8). When average May relative humidity was less than 54.5% and average May minimum temperature was less than -0.79°C all cases were negative for WPBR. When average May relative humidity was greater than or equal to 54.5% and average May precipitation was less than 87.875mm, there was a high probability (0.923) of presence of WPBR. The total misclassification rate for this tree was 10.5%, K=0.873, presence of white pine blister rust was accurately classified 96.4% of cases, and absence was correctly classified in 92% of cases. The classification tree model was used to predict presence / absence of WPBR on the 612 survey plots, 325 of which were used to develop the model. A t-test showed that modeled risk, or predicted presence of WPBR, was significantly higher ($p<0.0001$) on plots that currently have WPBR (n=312) than on plots that are currently uninfested (n=300).

The risk map developed from the classification tree model selected from PRISM and plot variables is shown in Figure 4.9. *Cronartium ribicola* is predicted to be present on approximately 597,350 ha of white pine stands according to the classification tree model. This represents approximately 49% of the area containing white pines in Colorado based on the white pine distribution layer developed. According to this model areas across the state are at risk for pathogen establishment. A close-up of the Roosevelt N.F. is shown in Figure 4.10 illustrating the predicted presence and absence of WPBR as well as the locations of survey plots and the actual presence or absence of WPBR. The compiled GIS white pine distribution layer was created by merging four separate sources of

information on the distribution of white pines and as such contains overlapping polygons. This resulted in areas on the risk map that predict both the presence and the absence of WPBR; these areas are depicted in olive green/brown on the classification tree model risk maps (Figures 4.9 and 4.10).

Disease Pressure

Two multiple linear regression models were created to explain the variation in disease pressure based on 15.24 cm canker bins (Table 4.3). In both models, number of years of exposure, which was determined by maximum canker length observed on a plot divided by the average canker growth rate of 8.4 cm (Kearns 2005, Chapter 3), is an important predictive variable. Not surprisingly, the longer the plot has been exposed to the pathogen, the more infection events have occurred. Other than the number of years of exposure, only meteorological variables were included to predict the disease pressure at a given site. Meteorological variables were significantly correlated with disease pressure (Table 4.4). No plot-level variables including *Ribes inerme* or stream density were selected in either of the models. Model 1, which explained 79.2% of the variance in disease pressure ($F=294.94$, $p<0.001$, error sum of squares (ESS) = 309.7) predicts that infection episodes increase with increasing precipitation and relative humidity in September, the time of year when infection by basidiospores likely occurs. Disease pressure also was predicted to increase with higher July maximum temperatures and decrease with higher June maximum temperatures and higher August relative humidity. Model 2 explained 78.9% of the variance in occupied canker bins ($F=291.2$, $p<0.0001$, ESS=312.9). In addition to predicting increasing infection events with increasing years

of exposure, this model predicted that disease pressure increases with September precipitation, June and September relative humidity, and increasing mean July/August/September maximum temperatures. The model also predicts that disease pressure declines with increasing August relative humidity.

The CART analysis (Figure 4.11) also selected years of exposure, September precipitation, and mean July/August/September maximum temperatures as important splitting criteria, but also included a plot variable in the proportion of the trees in the plot with DBH>15.5 cm. Disease pressure increased with years of exposure, greater September precipitation, and higher July/August/September maximum temperatures. Stands with higher proportions of larger diameter trees were predicted to be more likely to experience more infection episodes than stands with lower proportions of large diameter trees. The regression tree model explained 86.8% of the variance in number of occupied canker bins.

WPBR Hazard

Incidence

Multiple linear regressions produced two models to predict incidence of white pine blister rust (Table 4.5). The first model contains years of exposure, based on maximum canker length. The model was able to explain only 63.1% of the variation in incidence found on the 473 survey plots used to develop the model ($F=88.05$, $p<0.0001$, ESS=22.3) and contained nine variables. The first model suggests that incidence increases with more years of exposure and with higher proportions of larger diameter (>15.5 cm DBH) trees,

greater $\log_{10}$ density of *Ribes inerme* within 1km, June relative humidity, and higher mean May/June minimum temperatures. According to this model, incidence decreases with increasing September minimum temperature and mean May/June precipitation. The second model included our estimate of disease pressure, based on number of canker bins occupied and explained 66.2% of the variation in incidence among survey plots ($F=151.94$, $p<0.0001$, ESS=7.54). This model suggests that incidence increases with the number of infection episodes, the proportion of the stand with stem diameters greater than 15.5 cm, July/August/September mean minimum temperatures, June relative humidity. The model also indicates that incidence increases with cooler May/June minimum temperatures and on plots located at the bottoms of slopes (includes toe and foot slopes and valley bottoms).

The regression tree (Figure 4.12) selected by cross-validation explained 72.8% of the variation in incidence with nine terminal nodes and had a residual mean deviance of 0.0131. Incidence was related to years of exposure, when the years of exposure were less than 1.4, higher predicted incidence occurred on plots with longer median frost free periods. When years of exposure exceeded 1.4, the highest incidence levels were associated with warmer September minimum temperatures and low proportion of stems less than 5cm DBH (or conversely larger stem diameters). Slope position was also a splitting variable with plot located at the bases of slopes and at the summits having higher predicted incidence than those located on slope shoulders or midslope. Mean percent live crown for all trees on the plot less than 75% was associated with higher predicted

incidence than higher mean percent live crown. Percent live crown is related to stand density, with more dense stands creating shading that reduces the amount of live crown.

The classification tree for predicting categorical level of incidence (Figure 4.13) had four terminal nodes and a misclassification rate of 22.2%. Low level incidence (<25%) was correctly classified in 89.1% of cases, moderate incidence (25-50%) was correctly classified in 72.9% of cases, and high incidence (>50%) was never correctly classified. Of the 44 plots with incidence >50%, 93.2% were classified as moderate incidence with the remaining 6.8% classified by the model as low incidence. The classification tree has splits at years of exposure, September minimum temperature, and June precipitation. Apparently these three variables are not sufficient to explain differing levels of incidence.

Severity

The mean relative severity index (RSI) ranged from 0 to 6.5 with 90% of the 504 survey plots having a mean RSI of less than 2.5. The average RSI varied significantly among the 13 study areas (Table 4.6). The regression tree for predicting RSI minimized the deviance with 5 terminal nodes (Figure 4.14). Using years of exposure, September minimum temperature, and the average percent live crown for the plot, the tree was able to account for 58.6% of the variation in RSI. The model predicts that stands exposed for less than 1.1 years will have an average RSI of 0.08, and those that have been exposed to the pathogen between 1.1 and 3.4 years will have an average RSI of 0.85. When years of exposure exceed 3.4, the next criterion for splitting was September minimum temperature, with cooler sites averaging a lower RSI than those with warmer September

minimum temperatures. Years of exposure to the pathogen, September minimum temperatures in excess of 3.2°C, and mean percent live crown of less than 72.2 percent resulted in the terminal node with the highest mean predicted RSI of 2.84. This suggests that cooler September temperatures may be limiting the amount of disease. Although density of trees was not selected as a variable in the model, lower mean percent live crown is associated with denser stands, which during the daytime typically remain cooler and moister than open stands.

Discussion

This study has reinforced the view that modeling disease epidemics across vast landscapes is complex. Disease occurrence and incidence is influenced by environmental conditions controlled at synoptic, mesoscale, and microsite levels, host and pathogen dynamics, and time. In broad terms, the climate of the central Rocky Mountains is characterized by cold winters and dry, moderate summers (Whiteman 2000), and large-scale weather patterns that differ between the northern and southern portions of this study. The area east of the Continental Divide along Colorado's Front Range and into southern Wyoming experiences episodic humid air fronts in the spring and summer and up-slope and convective storms throughout the summer (Whiteman 2000, N. Doesken, pers. comm.). Areas east of the Continental Divide in northern Colorado and southern Wyoming experience much drier summers, receiving most of their moisture as snow in the winter (N. Doesken, pers. comm.). Areas west of the continental divide in southern Colorado experience relatively dry late spring and early summer conditions and beginning in late July receive monsoons that can result in heavy afternoon rain events

(Whiteman 2000). Jacobi et al. (2002) examined the influence of synoptic and mesoscale weather systems on the frequency of comandra blister rust infection episodes in three study areas in Wyoming (Shoshone N.F. and Medicine Bow N.F.) and southwestern Montana. Across that geographical range, only 3% of systems occurred at all three study areas, 19% reached two of the three, and the remaining 78% of systems were recorded in only one area. They concluded that the frequency of infection episodes was related to prevailing summer weather patterns that differed between regions of the central Rocky Mountains (Jacobi et al. 2002). The data on which our models were developed cover a much broader geographic area from the Shoshone N.F. and Wind River Range in Wyoming, across the Great Divide Basin to the Green and Shirley Mountains, east to the Laramie Mountains, south to the Medicine Bow Mountains into Colorado, then extending south to the Sangre de Cristo Range and Wet Mountains of southern Colorado.

In the generally arid central Rocky Mountains, moisture may often be a limiting factor in the spread and establishment of WPBR. For example, during the extremely dry 2002 field season no *C. ribicola* infections were found on *Ribes* hosts on over 600 WPBR and extensive *Ribes* survey plots. Temperatures may also be limiting, either by being too cool in the late spring/early summer for aeciospore production and germination and in August and September when basidiospores are produced or too hot in July and August when teliospores are being produced. The climate data (PRISM) used to develop these models represents 30 year (1961-1990) monthly averages. The pathogen does not sporulate, disseminate, and infect its hosts under monthly average conditions, rather it responds to distinct weather events with suitable temperatures and high available

moisture. Even so, the models developed here show that there is a correspondence between monthly average climate and the short-term weather events that promote infection of pines by *C. ribicola*. A study of weather station data from the RAWS (remote automated weather station) network and on-site weather stations placed in limber pine stands throughout central and southeastern Wyoming and Colorado to determine the co-occurrence of favorable conditions in late spring and late summer is underway (W.R. Jacobi and A.E. Goodrich, pers. comm.). Knowledge of the locations in which suitable conditions occur and the frequency of infection-favorable events should allow for further calibration of the models developed herein.

Occurrence and incidence of plant disease are also determined by the interactions between hosts and pathogens. The genetics of the host pine may confer some level of resistance to the rust pathogen. There is evidence of a gene-for-gene relationship between host resistance alleles and pathogen virulence alleles in the WPBR pathosystem. The white pine blister rust gene-for-gene system is comparatively simple with only a few major resistance genes (Cr) discovered so far (Kinloch and Dupper 2002). Recent studies have indicated that major gene resistance is present in populations of southwestern white pine and limber pine (Kinloch and Dupper 2002). While the Cr genes are very effective, they are vulnerable to the avirulence genes of the pathogen (Kinloch et al. 1999). Inocula from various locations have been shown to neutralize resistance alleles in both sugar pine and western white pine (Kinloch and Dupper 1999, Kinloch and Dupper 2002). Plant pathogens can adapt to different environmental and host conditions creating epidemiological fitness phenotypes that exhibit differing ability to cause disease

(McDonald 2000). Genetic variation in epidemiological fitness has been shown for *C. ribicola* (McDonald and Andrews 1982). The genetics of *C. ribicola* populations in the central Rocky Mountains are currently unknown, but it is certainly feasible that some adaptation has occurred. Kimmey and Wagener (1961) reported that, unlike reports from the Lakes States (Van Arsdel et al. 1956) temperatures above 24°C do not have a limiting effect on teliospore viability in California. It is possible that the pathogen has shifted its epidemiological requirements to accommodate the warmer and drier climate of the central Rocky Mountains.

Since its introduction in 1910 to western North America, *Cronartium ribicola* has spread through many of the West's susceptible white pine populations. The moving front has progressed from the area near Vancouver, British Columbia where the pathogen was initially introduced, to the south and east and is now located in northern Colorado. Disjunct populations also exist in New Mexico (Hawksworth 1990), South Dakota (Lundquist et al. 1992), and the Wet and Sangre de Cristo Mountains of southern Colorado (Blodgett and Sullivan 2004). Any attempt to examine the epidemiology of plant diseases must contain a temporal component to determine why there are variations in levels of infestation. Previous studies have indicated that there is a progressive intensification of WPBR with time (Lachmund 1934, Fracker 1936, Conklin 2004). The length of time the pathogen has been present, established, and affecting white pines in the central Rocky Mountains has not been definitively established. Our approach to resolve this problem was to measure canker lengths and calculate a mean canker growth rate using dendrochronological techniques (Kearns 2005, Chapter 3). Due to interacting

factors involving WPBR epidemiology and meteorology, including the lag period between infection and canker development (Lachmund 1933) and the inactivation of cankers (Kimmey 1969) the reconstruction of potentially fifty years or so of infection histories is complicated and based on the current availability of cankers.

In spite of these limitations, some advanced knowledge of the types of sites that promote infections by *C. ribicola* could be used by land managers to coordinate and prioritize monitoring and, if necessary, control efforts. We modeled the risk of WPBR by examining relationships between the presence/absence of WPBR and plot and meteorological variables. The preliminary model, based on data commonly available in USDA Forest Service databases and assumptions derived from models developed in other regions, was not effective in predicting the risk or hazard of WPBR in the central Rocky Mountains. Although incidence was significantly higher on plots categorized as high hazard by the preliminary model, there were no significant differences in the incidence of disease on what were predicted to be moderate and low hazard sites. The model also could not accurately predict where WPBR was likely to occur. Several of the assumptions in the preliminary model were contradicted by collected survey data. For example, the risk of WPBR was assumed to be low in ponderosa pine forests due to these forest's prevalence on hotter, drier sites. However, we found a significantly higher incidence of WPBR on sites with a component of ponderosa pine (Kearns 2005, Chapter 1). Survey data also indicated that incidence of the disease was related to elevation and topographic position, but was not significantly related to aspect or slope percent (Kearns 2005, Chapter 1). The preliminary model developed by Geils et al. (1999) to predict

hazard of WPBR infection in southwestern white pine in New Mexico provided reasonable accuracy when compared to data collected on incidence and severity of WPBR in plots within each of the three defined hazard zones. There was no attempt, however, in that study to use the model to predict the risk of WPBR establishment. Our results suggest that the preliminary model could be adjusted to local conditions in areas in which the pathogen has already become established, to predict the type of sites with the highest level of hazard. However, the preliminary model can not be accurately applied to predict where on the landscape that pathogen is likely to establish new infestations.

Three different models were developed to predict risk of WPBR establishment on a site. The logistic regression model indicated good agreement between actual and predicted presence/absence of WPBR. When the model was tested against plots in southern Wyoming and Colorado, plots that are currently infested had significantly greater predicted probabilities of presence of WPBR than did plots that are currently uninfested. There was also a significant positive correlation between mean predicted probability by study area and the current proportion of infested plots. However, it was clear that plots located in the Sangre de Cristo Mountains had a much higher proportion of infested plots than the logistic model predicted. Those plots are located in the vicinity of Mosca Pass, which contains populations of both limber and Rocky Mountain bristlecone pine and is uniquely situated among very dense populations of *Ribes inerme* and topographically located along a narrow valley. It is in this area that the first natural infection of WPBR on Rocky Mountain bristlecone pine was reported (Blodgett and Sullivan 2004). These

plots were located in a very small sample area, and it is likely that plots located over a larger geographic area would have a lower proportion of plots infested.

The inclusion in the model of variables relating to May and September relative humidity support the reported epidemiological requirements of the pathogen for free water or high relative humidity for the aecial, telial, and basidial stages. As mentioned above, the average monthly humidity probably provides an inaccurate measure of conditions conducive for the production and germination of spores, but sites with higher average relative humidity are likely those that more frequently reach the high levels of relative humidity required by the pathogen. Stream density is related to the distributions of at least two species of *Ribes* found in Wyoming and Colorado. According to the results of *Ribes* surveys, densities of both *R. inerme* and *R. lacustre* were significantly greater in riparian areas and odds of the presence of those species increased nearly 11 and 18 times, respectively in riparian areas compared to limber pine forests (Kearns 2005, Chapter 2).

The CART analyses for predicting risk of WPBR proved very interesting in that when provided the full complement of both plot and meteorological variables, only the meteorological variables were selected. The tree created with the plot variables alone had a lower agreement between predicted and actual presence of WPBR than did the tree that selected only meteorological variables. Still, the probability of WPBR was greatest on sites with greater *R. inerme* densities and greater stream densities. Both of these variables are based on the area surrounding the plot within a 1 km radius. This seems to indicate that the presence WPBR is not restricted to sites on which white pines grow

amidst *Ribes*, rather the presence of *Ribes* in the vicinity of white pines is also of importance. This is also supported by the presence of cankers throughout the crowns of affected trees, which suggests that longer distance transport of basidiospores may be taking place. The model based solely on meteorological variables selected three variables relating May climate conditions as providing the best splits of the data. Highest predicted occurrence of WPBR occurred when average May relative humidity exceeds 54.5% and either mean May precipitation is low or August mean minimum temperatures are greater than 8.8°C. High levels of precipitation in May may wash aeciospores out of air currents or off the *Ribes* host and prevent their dissemination to or infection of *Ribes* leaves. Mean monthly temperature minimums were regarded as representing mean monthly nocturnal temperatures (Charlton 1963), which at extremes may limit the production and germination of teliospores and basidiospores. Although only 24 cases were split at the August minimum temperature node, the 12 with temperature greater than 8.79°C had a 100% probability of being infested with WPBR. This may provide an indication that low nighttime temperatures may restrict the distribution of the pathogen, but further epidemiological studies on the races of the pathogen present in the central Rocky Mountains need to be completed before that is substantiated. That there were highly significant differences in mean predicted risk of WPBR between currently infested stands and uninfested stands when the model was tested on plots including the supplemental survey plots in Colorado is promising. This model may have applicability in predicting the risk of WPBR in Colorado's native white pine populations.

Mapping risk of WPBR to Colorado's white pine populations resulted in very different estimates of area of white pines at risk. The logistic regression model was much more restrictive and predicted many fewer hectares of white pines at risk compared to the CART model. Both models, while developed using plot data from Wyoming, predicted higher average probability of WPBR on plots in both Wyoming and Colorado that currently have WPBR, which indicates that these models are both applicable to Colorado's white pines. Both models predict that *Cronartium ribicola* will continue to expand its current distribution. One of the limitations to these risk maps is the white pine distribution layer, which does not capture the complete distribution of white pines in Colorado. As such, these maps provide a basis for establishing monitoring locations, but do not provide information on the ultimate distribution of *Cronartium ribicola* in Colorado.

Disease pressure, or the number of times a site has experienced infection events, is intimately linked to the number of years the site has been exposed to the pathogen. The longer the exposure the more likely that conducive meteorological events will have occurred. The multiple regression models and the CART analysis used years of exposure and various climatic variables to predict disease pressure. In addition to years of exposure, September precipitation was selected in all three models, with predicted disease pressure increasing with increasing September precipitation. Warmer maximum temperatures in July or the average of July/August/September maximum temperatures were associated with greater disease pressure, which contradicts epidemiological studies in the Lakes States where higher temperatures reduced the fertility of teliospores (Van

Arsdel et al. 1956). None of our sites had average maximum temperatures in excess of 35°C, which has been reported to completely prevent the formation of teliospores (Van Arsdel et al. 1956), but mean maximum July temperatures did reach 27.9°C on some plots. Before any accurate prediction of disease pressure can be made for sites in the central Rocky Mountains, further epidemiological analyses should be conducted to determine if the pathogen has adapted its life cycle to accommodate the different climatic regimes present here.

The multiple regression models and regression tree suggest that years of exposure is important when trying to predict incidence. Several researchers have shown that incidence increases with time. This relationship apparently holds true in the central Rocky Mountains. Incidence was also predicted by all three models to increase with larger stem diameters, which is likely a reflection of the increased target size of larger diameter trees and the higher probability of cankers on trees in larger diameter classes (Kearns 2005, Chapter 1). The first regression model predicted that incidence would increase with declining September minimum temperatures, but the opposite relationship was predicted in the regression tree model. In the second multiple regression model, we replaced years with disease pressure, which resulted in a slightly higher ability to explain the variation in incidence. However, the utility of this model in predicting incidence is limited because prior knowledge of disease pressure is required. Plots located at the bases of slopes had a higher predicted incidence than those located elsewhere, which may be related to diurnal winds patterns in which cooler air flows into valleys and slope bases at night (Whiteman 2000, Van Arsdel 1961). The regression tree model also predicted

that incidence would be higher at both slope bases and the tops of slopes compared to midslope or shoulder positions, which is supported by the cooler air found along ridge tops relative to those along the slope (Whiteman 2000). In all, the models developed to predict incidence were not able to explain a significant proportion of the variability in incidence found across these study areas and should only be used with extreme caution.

Smith and Hoffman (2001) modeled categorical incidence of WPBR in southern Idaho and western Wyoming using elevation, average stem diameter, mean summer precipitation, slope percent, habitat type, topographic position, stand density, and the presence of Ribes species. They were able to correctly classify 76% of plots into three levels of incidence using nine variables. Our attempts at the categorical classification of incidence were not very successful as no cases were predicted by the model to have incidence greater that 50%. The model does suggest, however, that the level of incidence increase with years of exposure, with warmer September minimum temperatures, and with higher levels of precipitation in July.

Our attempts to model relative severity index were not very successful. The regression tree model that minimized deviance could only explain 58.6% of the variation in relative severity index. Predicted RSI increased with longer exposure to the pathogen and warmer September minimum temperatures. The highest predicted mean RSI was in stands with an average percent live crown less than 72.2%, with mean minimum September temperatures greater than 3.19°C, and exposure to the pathogen greater than 3.4 years. RSI may be related to lower average percent live crown in that dense stands

may be cooler and moister. Lower mean percent live crown could also indicate the presence of understory and intermediate canopy level trees, which are by definition shaded by overstory trees resulting in lower percent live crown. The trees are also typically smaller in diameter and would thus rank higher on the RSI scale.

The objectives of this study were to create models to predict the risk and hazard of WPBR to Colorado's native white pines. The risk models show the greatest potential for use in determining where in Colorado we can expect WPBR to become established. Forest land managers can utilize the risk maps in concert with the models to prioritize monitoring , management, and, if necessary, control efforts. When the pathogen becomes established in an area, the infestations can be followed through time, which should allow for better calibration of the disease pressure and hazard models. Necessity of control will be determined by the projected impacts of the disease (Lundquist 2005). White pine blister rust can reduce regeneration of white pines by girdling cone-bearing branches or through direct mortality of seedlings. White pine blister rust can also result in the death of mature trees through the girdling of main stems, or the killing off of individual branches by profuse branch cankers (Lachmund 1934). As such, WPBR can affect species diversity and alter successional pathways and spatial distributions of hosts (Castello et al. 1995). These alterations may impact ecosystem functions including nutrient cycling and hydrologic regimes, or the provision of food and habitat for wildlife. By monitoring areas with the greatest likelihood of pathogen establishment, control measures can be applied where impacts of WPBR create conditions outside the desired range.

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Figure 4.1. Location of white pine blister rust survey plots in central and southeastern Wyoming and Colorado.

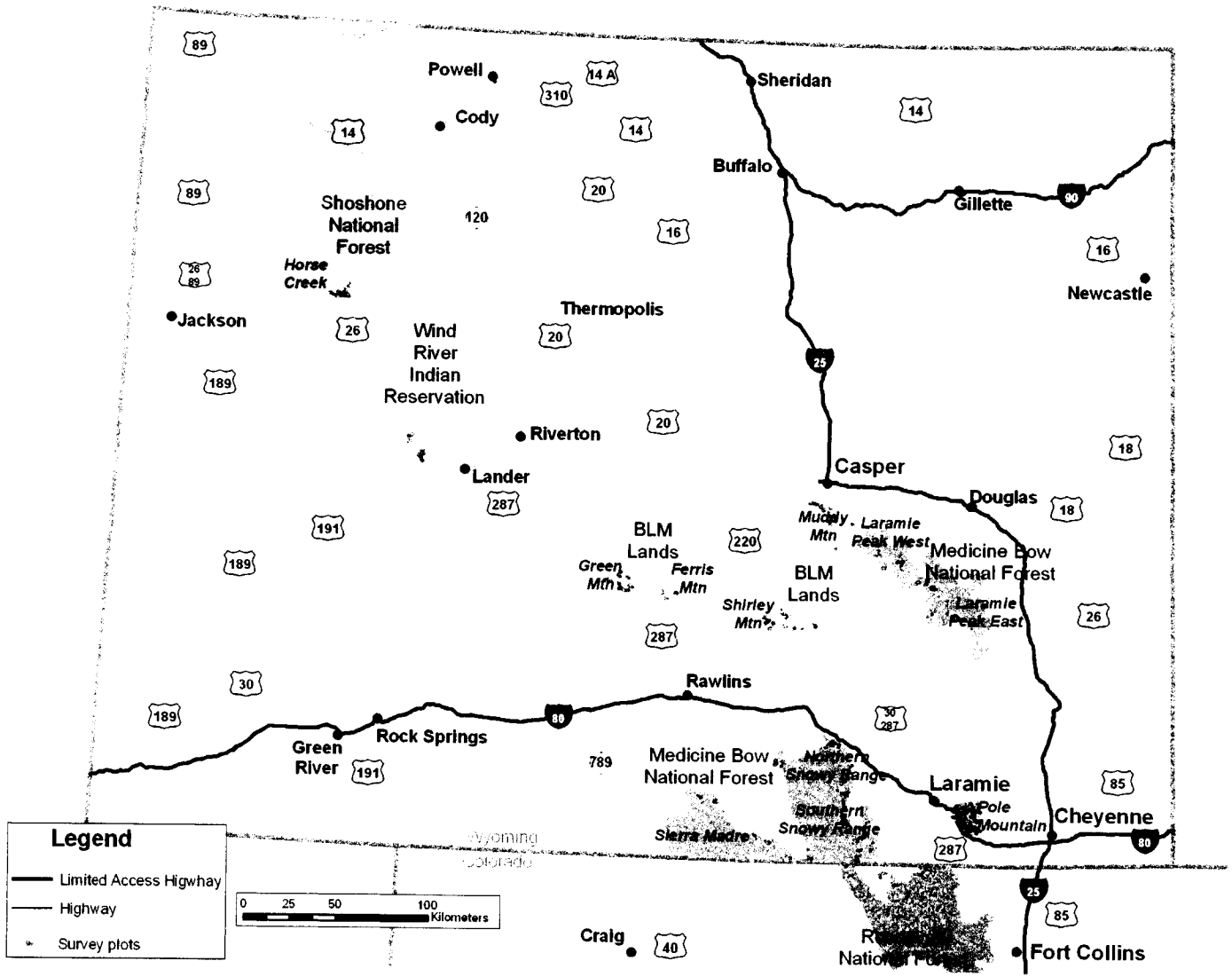


Figure 4.2. Location of supplemental survey plots in Colorado. Only those plots in areas with WPBR were used to evaluate developed risk models.

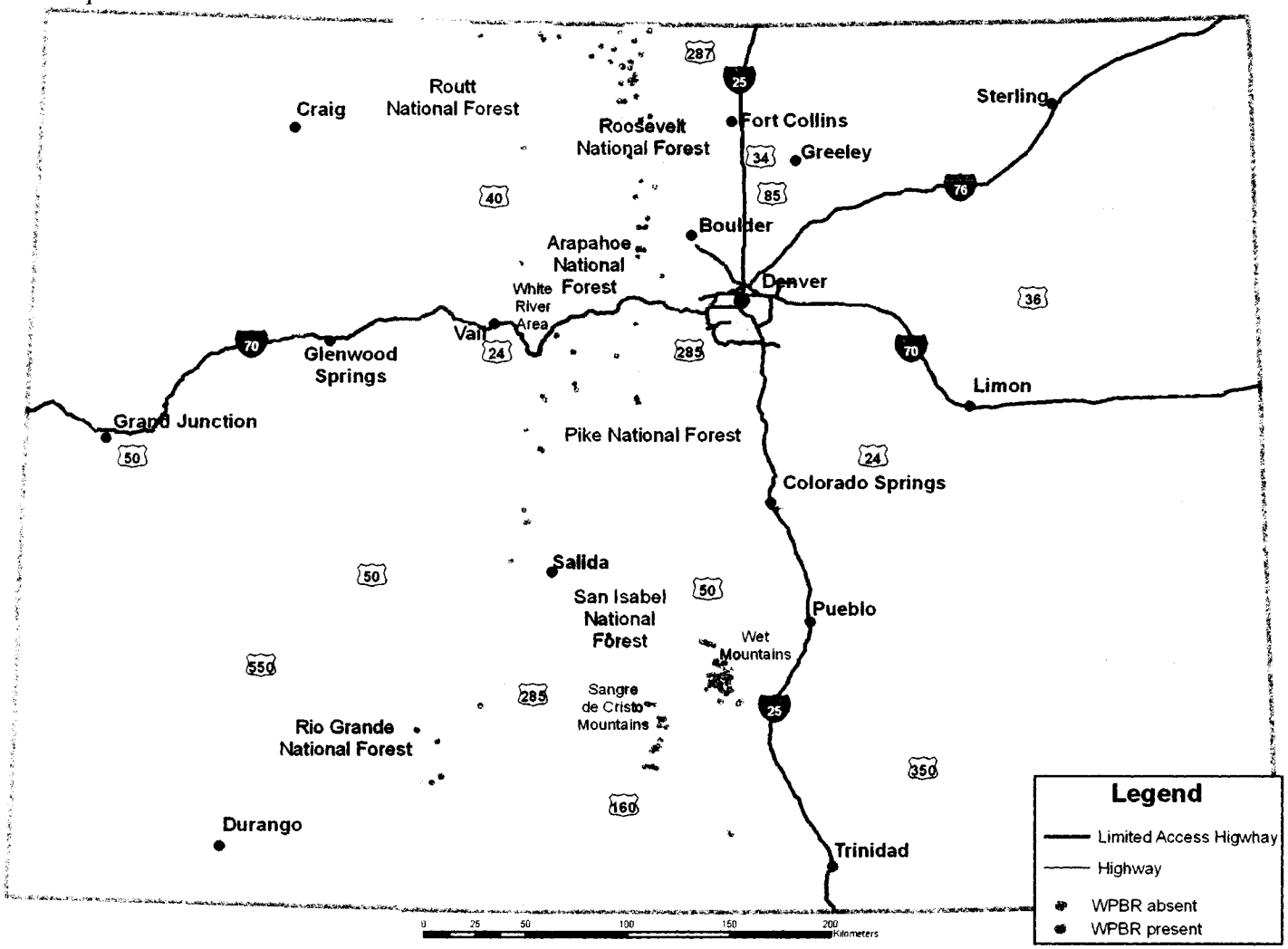


Figure 4.3. Receiver operating characteristic (ROC) curve for white pine blister rust risk logistic regression model.

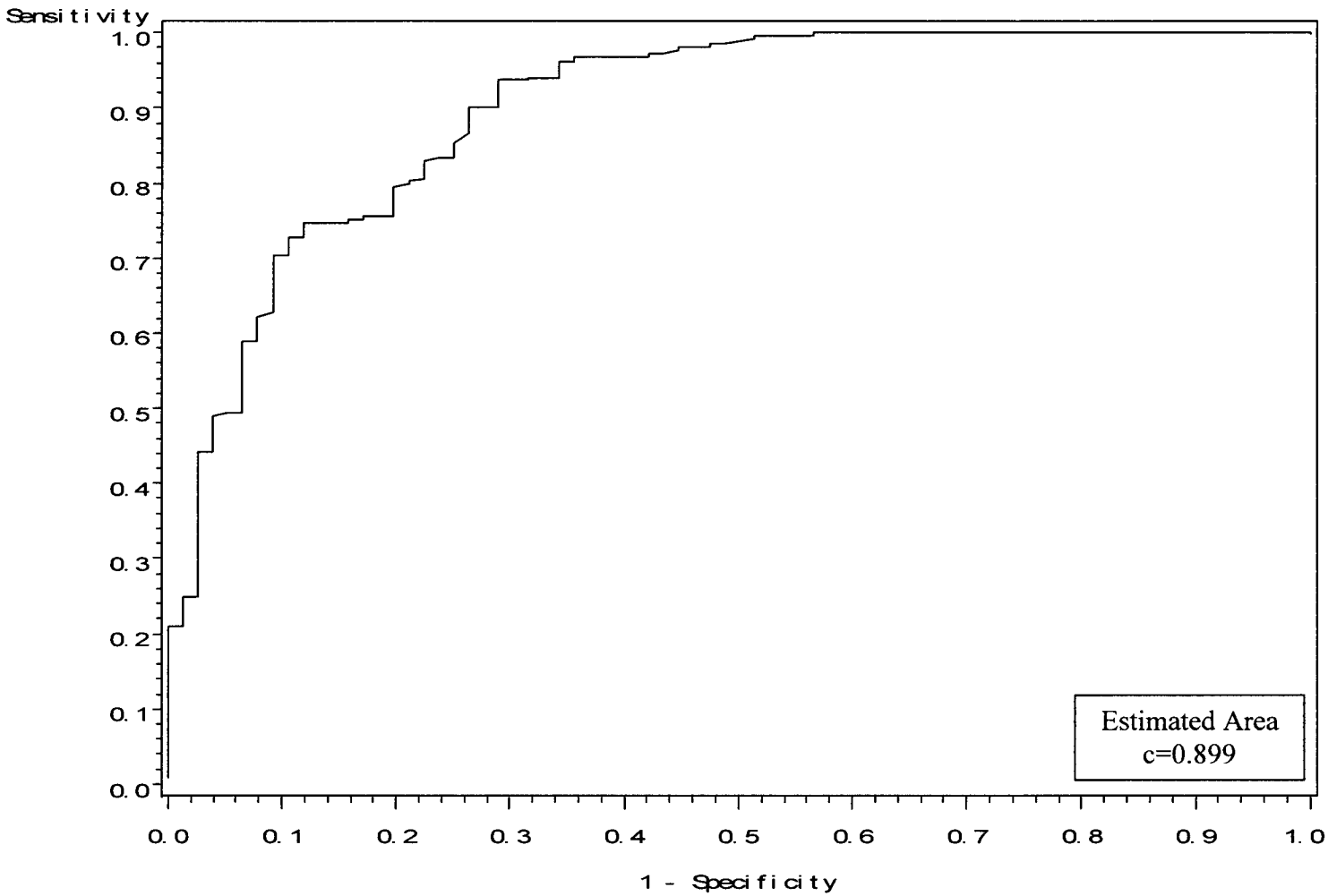


Figure 4.4. Relationship between observed proportion of plots infested and mean predicted probability of white pine blister rust for 16 study areas in central and southeastern Wyoming and Colorado.

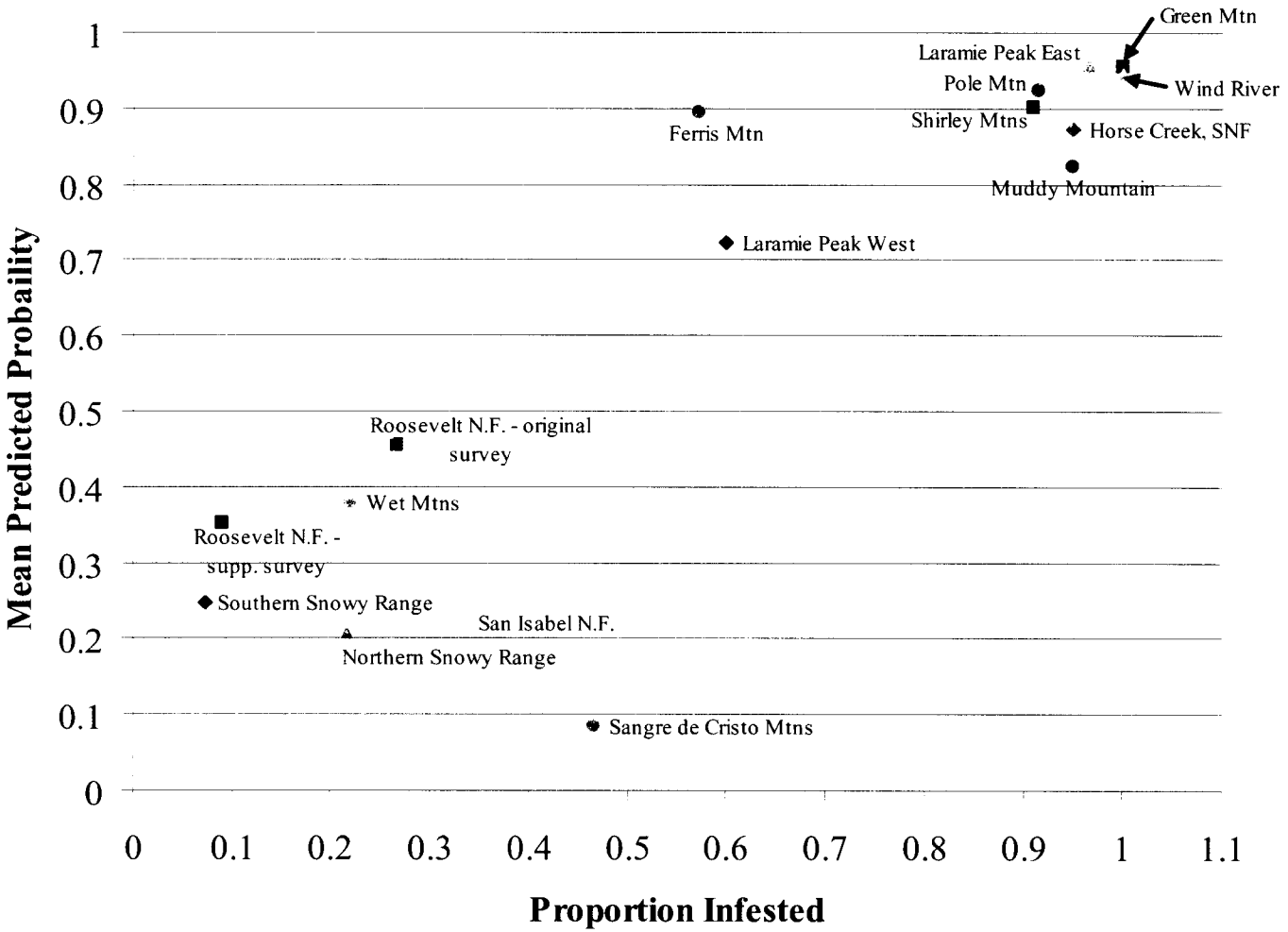


Figure 4.5. Map illustrating modeled risk of establishment of *Cronartium ribicola* in Colorado white pine stands based on the logistic regression model.

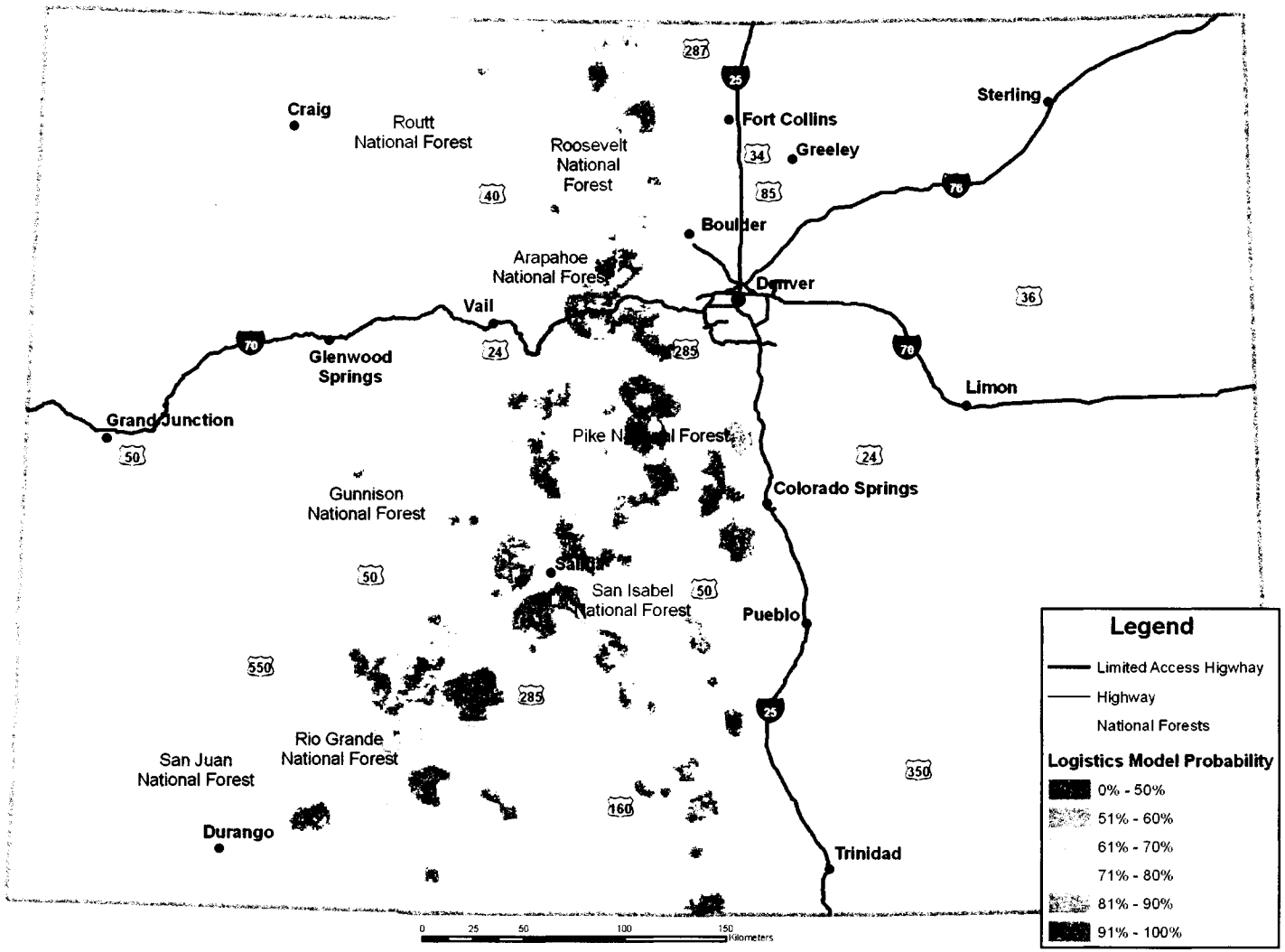


Figure 4.6. Map illustrating modeled risk of establishment of *Cronartium ribicola* based on the logistic regression model for the Roosevelt National Forest and the location of survey plots.

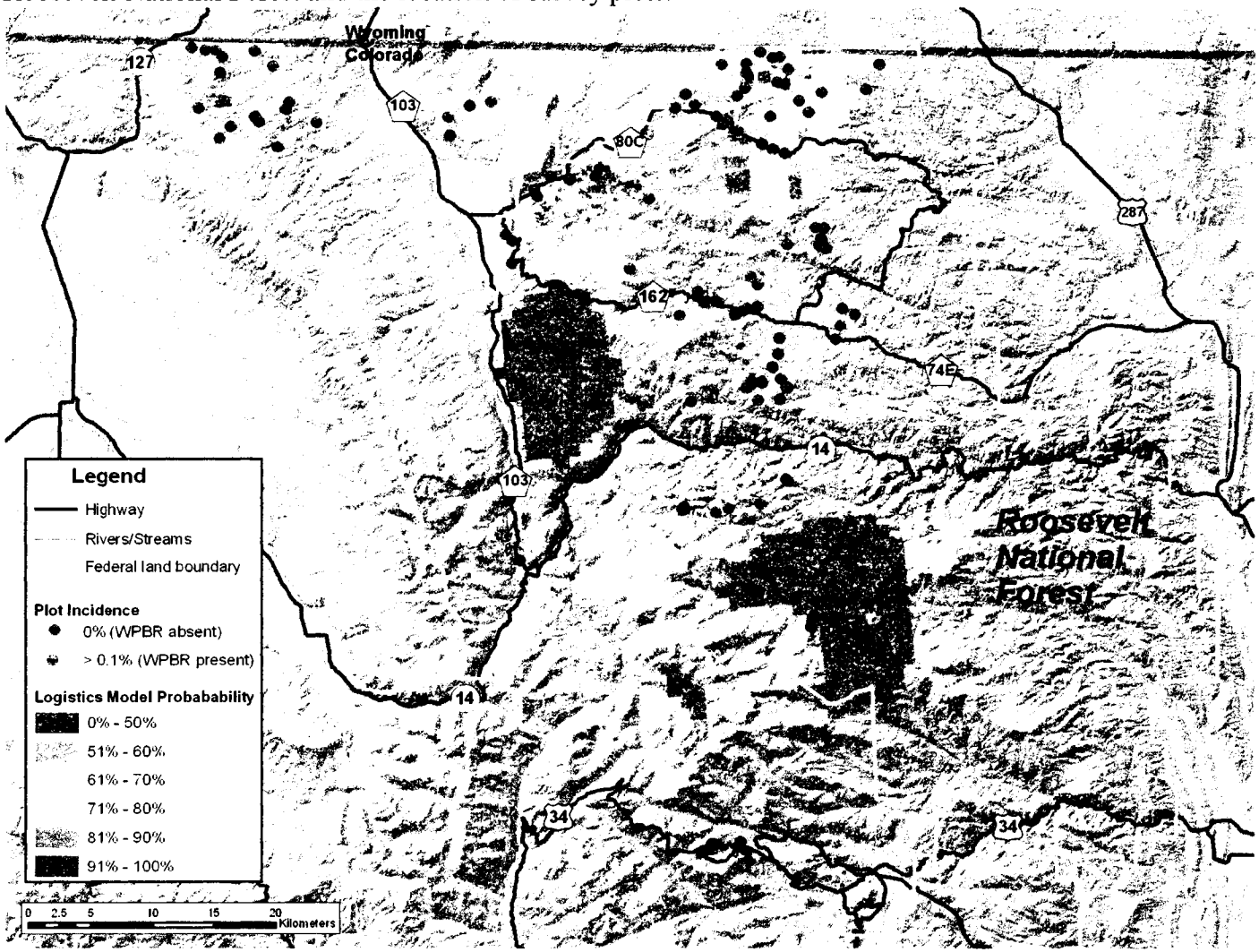
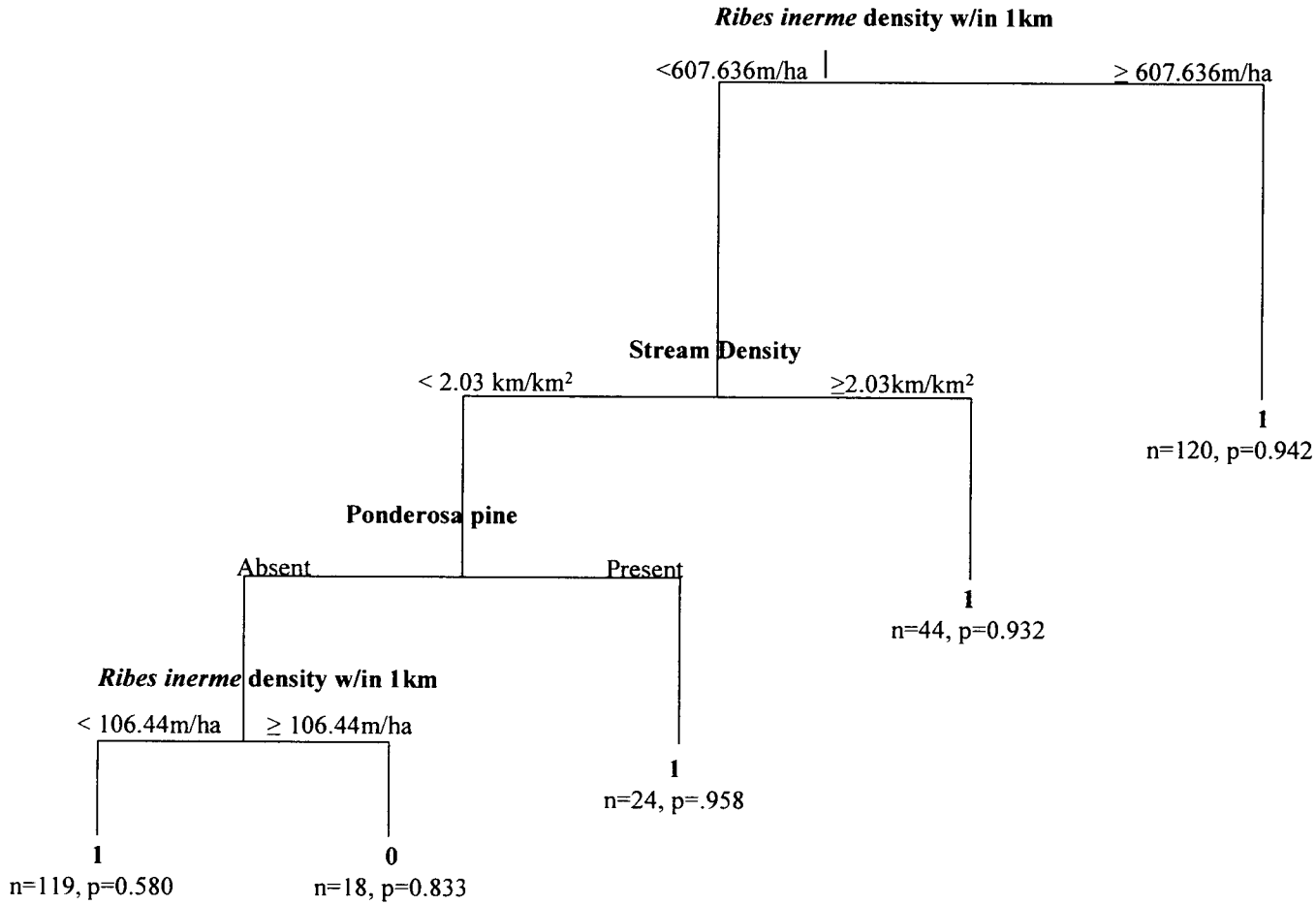
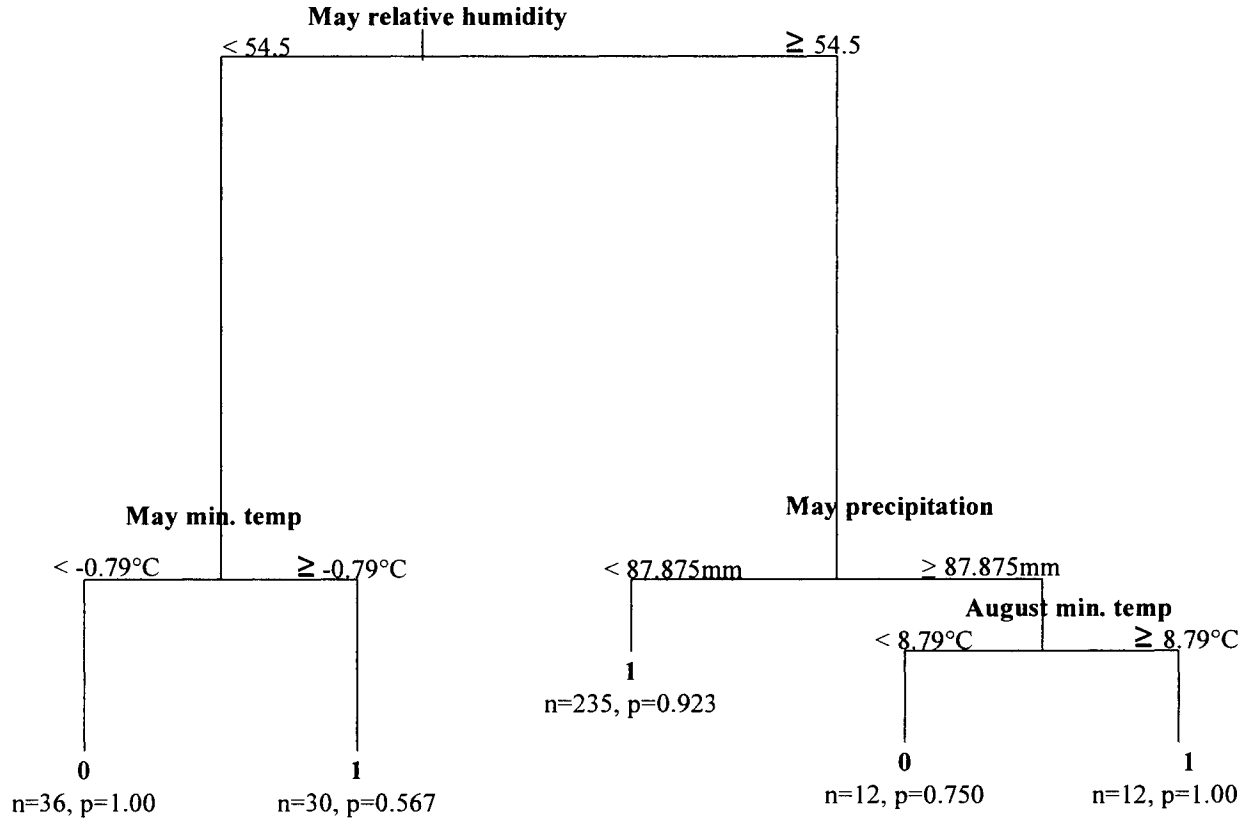


Figure 4.7. Classification tree for predicting presence/absence[1] of white pine blister rust based on plot variables.



[1] Presence of white pine blister rust coded as 1 and absence coded as 0. P represents the probability of membership in the specified WPBR class, n represents the number of cases placed in each terminal node.

Figure 4.8. Classification tree for presence/absence[1] of white pine blister rust based on both plot and meteorological variables.



[1] Presence of white pine blister rust coded as 1 and absence coded as 0. P represents the probability of membership in the specified WPBR class, n represents the number of cases placed in each terminal node. Meteorological data from PRISM represents 30-yr monthly averages.

Figure 4.9. Map illustrating modeled risk of establishment of *Cronartium ribicola* in Colorado white pine stands based on the classification tree model.

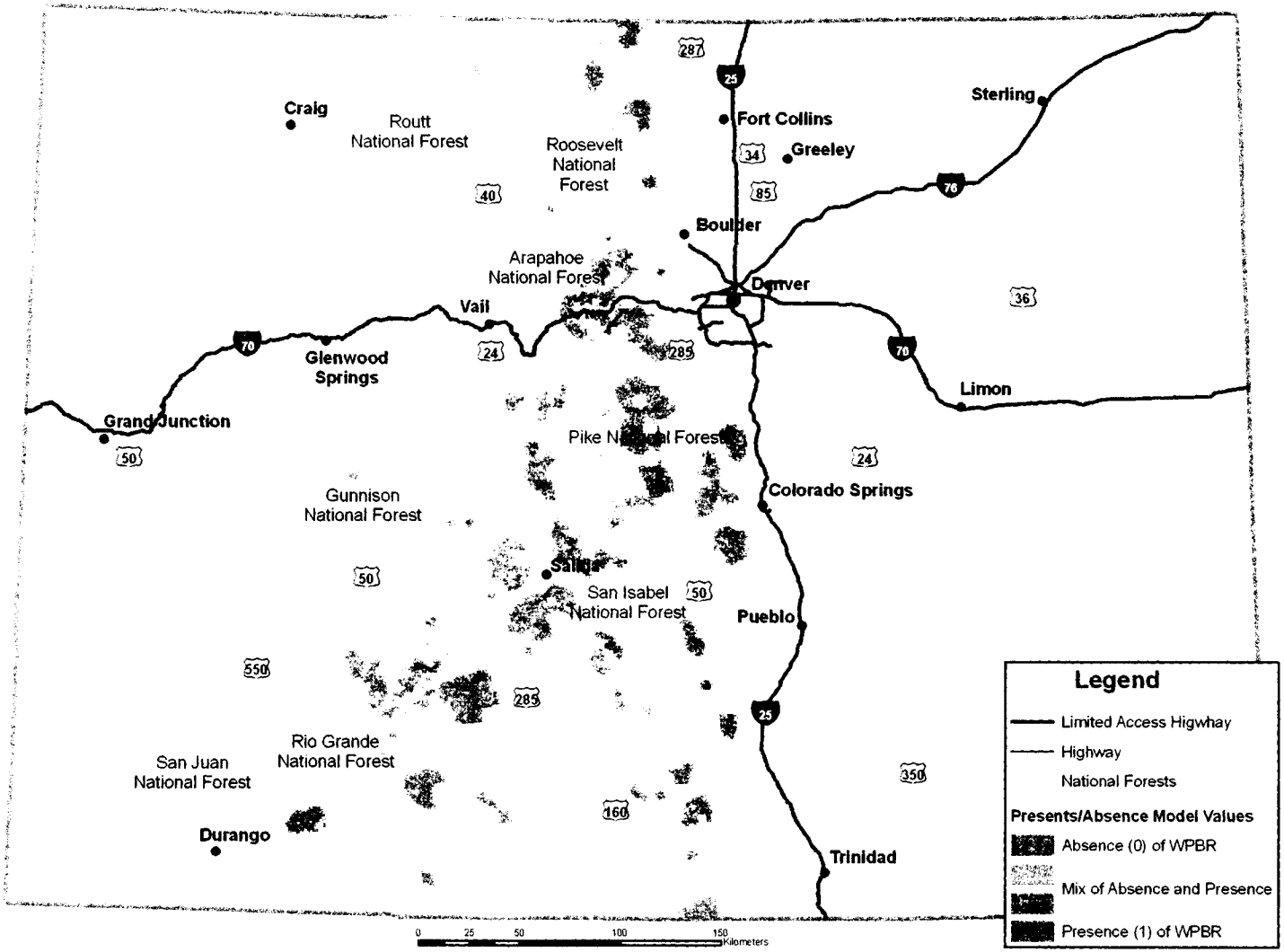


Figure 4.10. Map illustrating modeled risk of establishment of *Cronartium ribicola* based on the classification tree model for the Roosevelt National Forest and the location of survey plots.

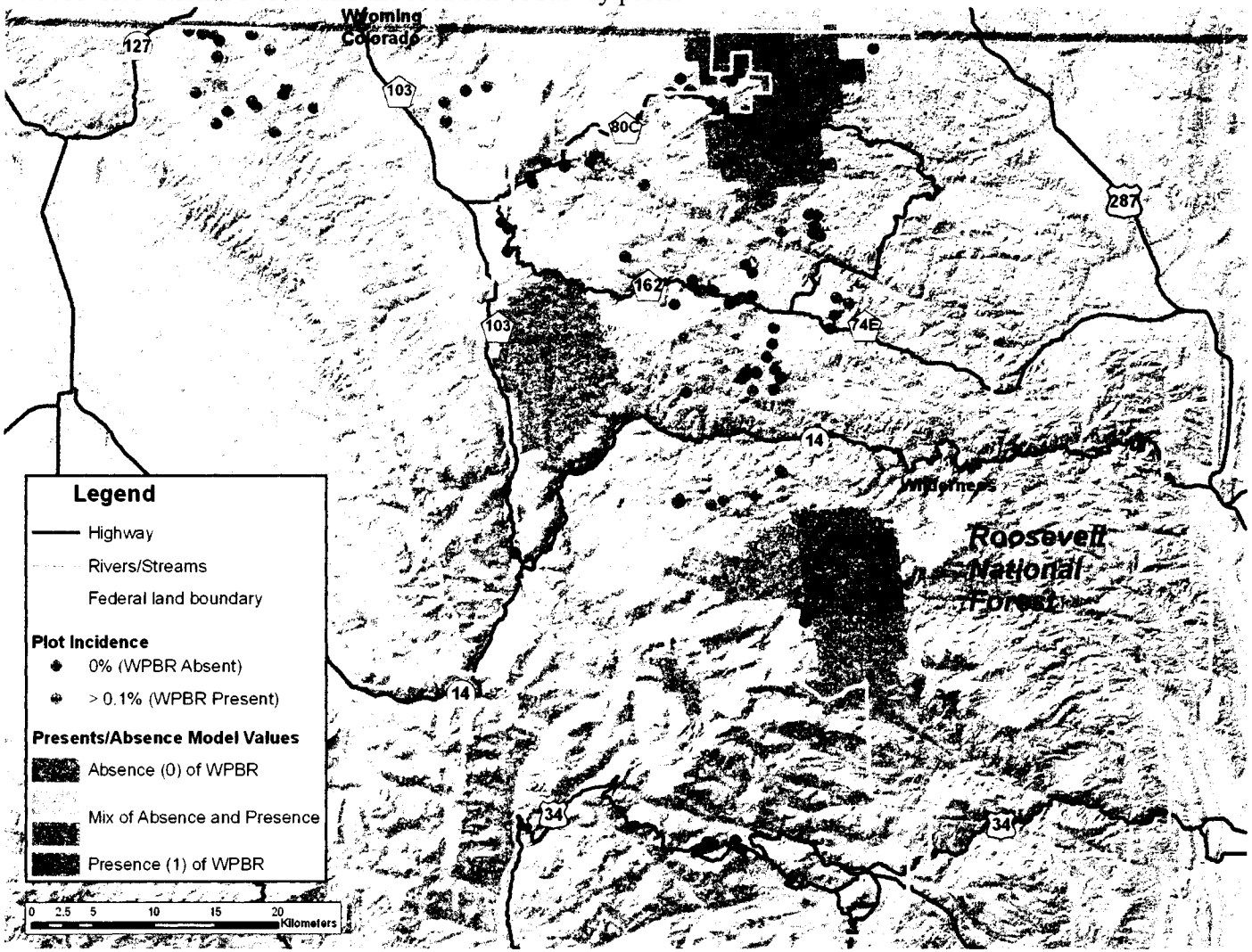
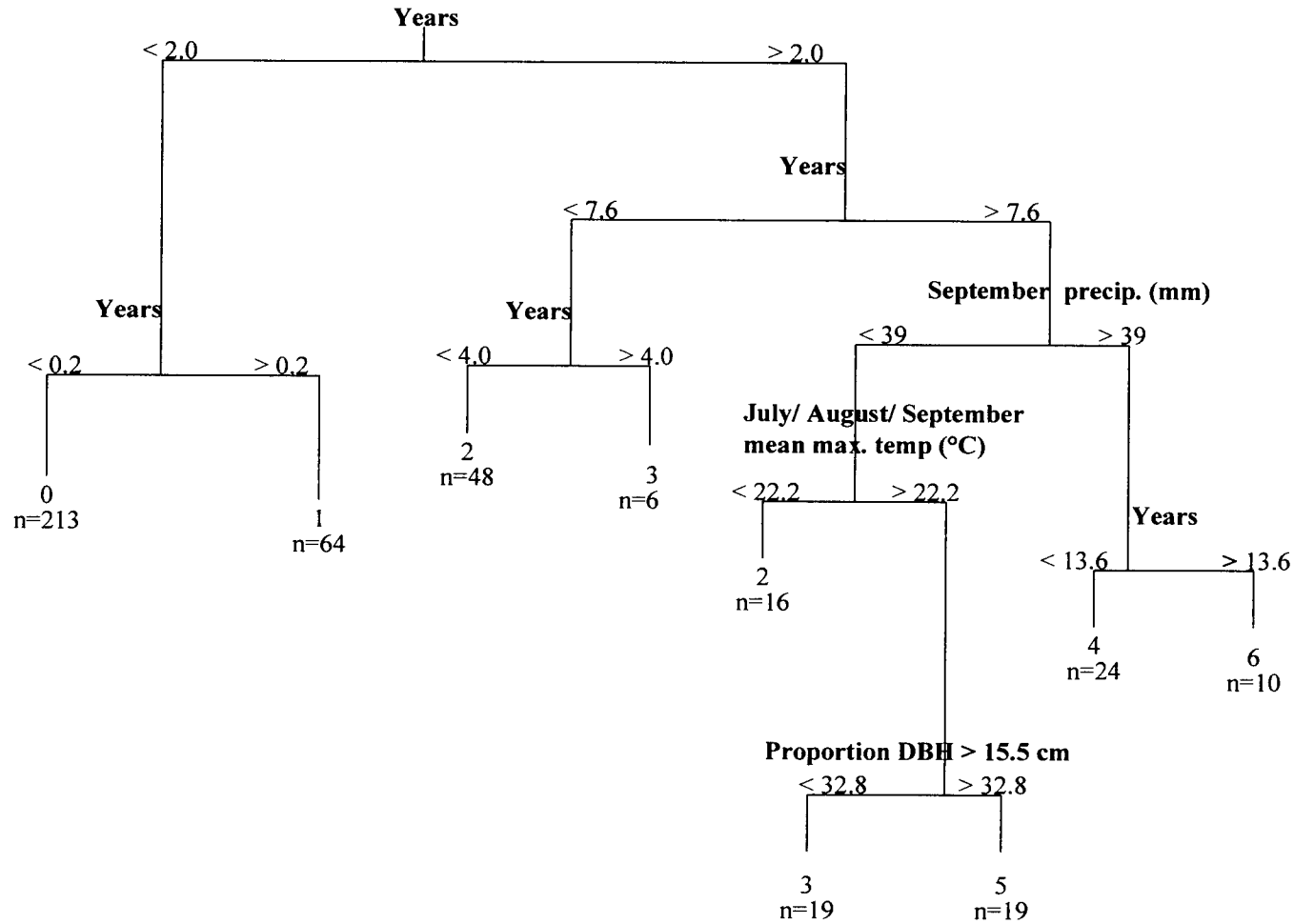
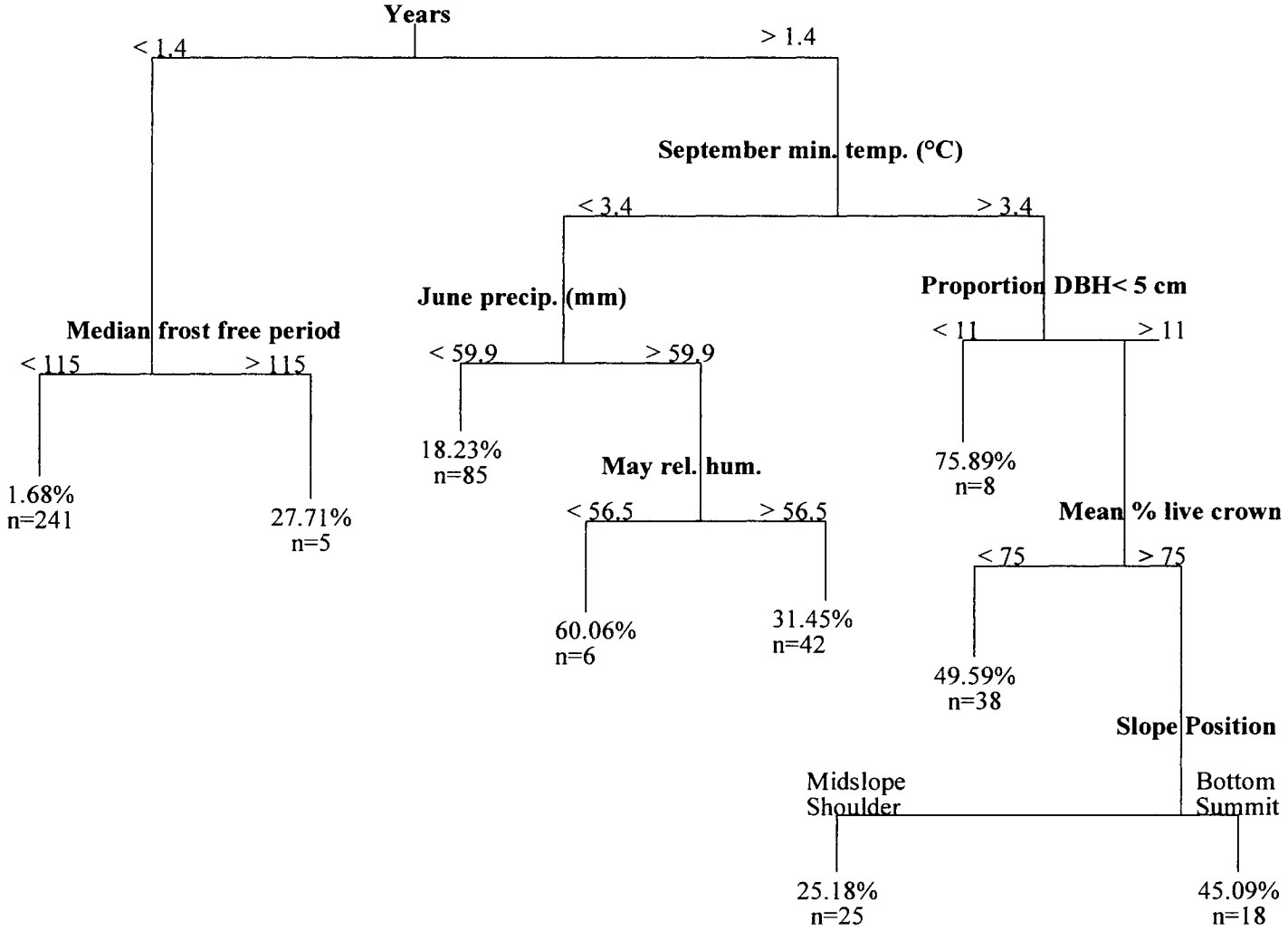


Figure 4.11. Regression tree for predicting the number of white pine blister rust canker bins[1] occupied, a surrogate for disease pressure.



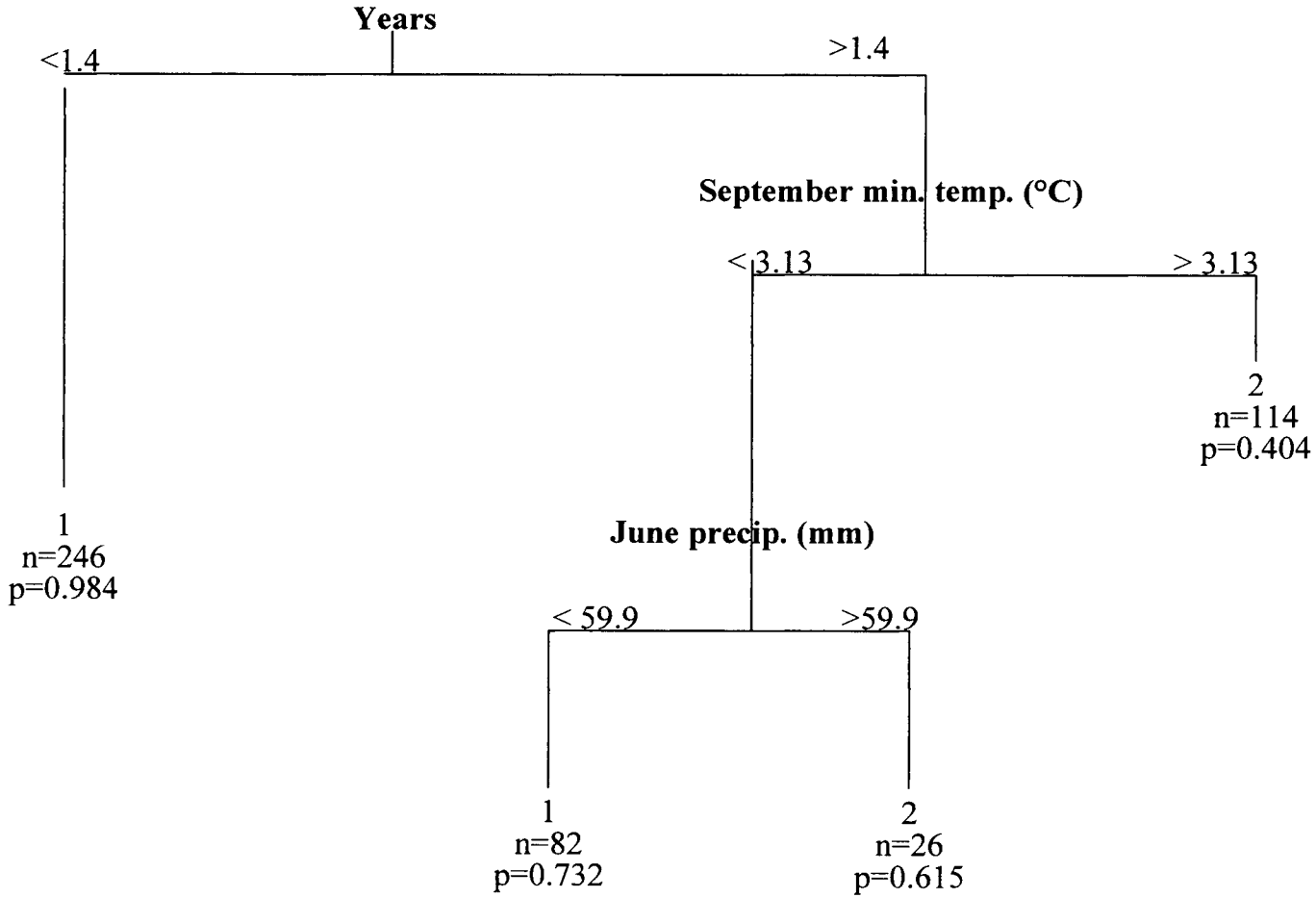
[1] Terminal nodes represent the number of predicted occupied canker bins (based on 15.24 cm canker size classes), n represents the number of cases placed in each terminal node.

Figure 4.12. Regression tree for predicting the incidence of white pine blister rust[1]



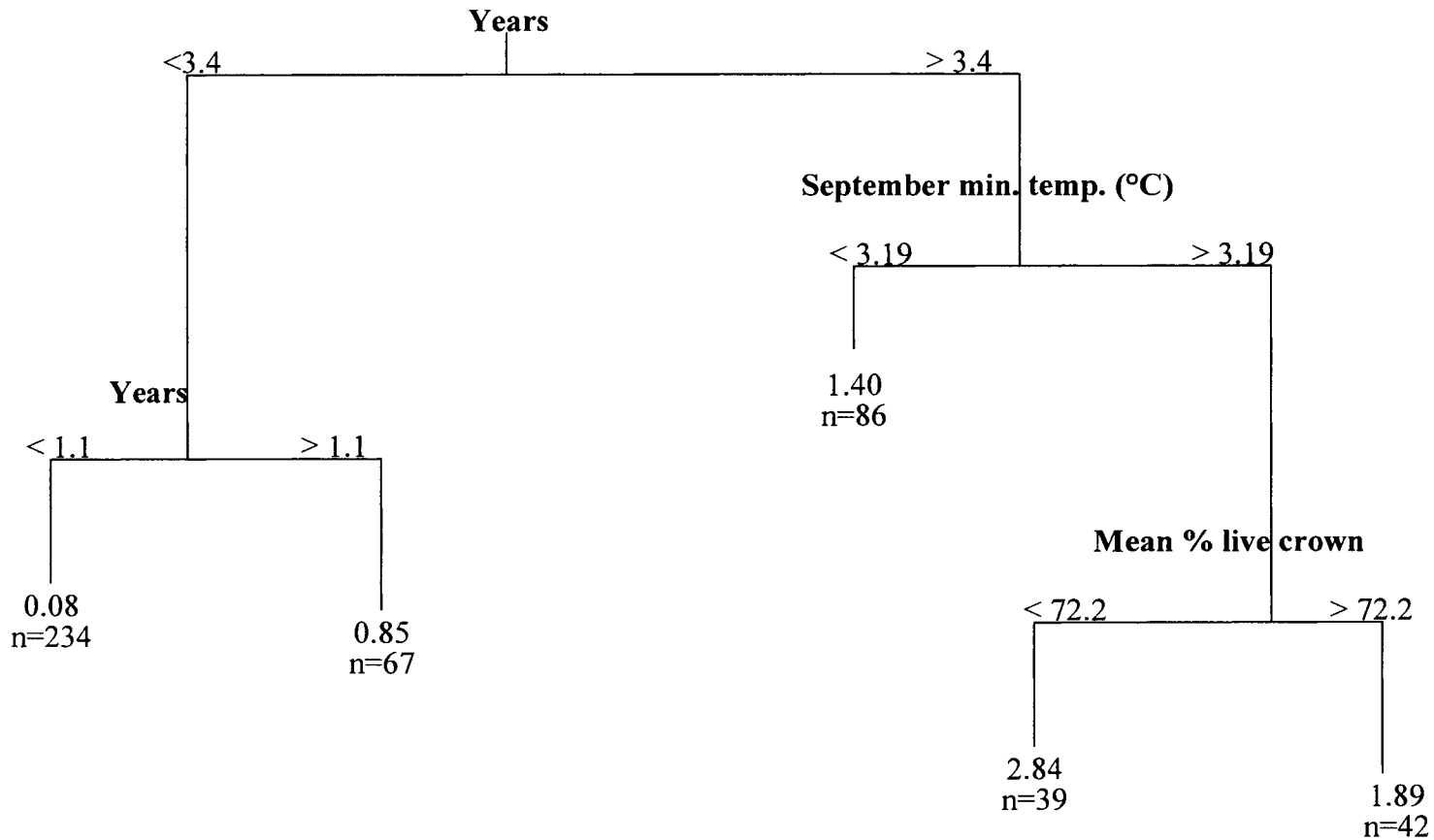
[1]Terminal nodes represent the mean predicted incidence, n represents the number of cases placed in each terminal node.

Figure 4.13. Classification tree for predicting the categorical incidence of white pine blister rust[1]



[1] Categorical incidence of white pine blister rust (1 is <25% trees infected, 2 is 25-50% trees infect, 3 is >50% trees infected). P represents the probability of membership in the specified incidence category; n represents the number of cases placed in each terminal node.

Figure 4.14. Regression tree for predicting the relative severity index for white pine blister rust[1]



[1]Terminal nodes represent the mean predicted relative severity index, n represents the number of cases placed in each terminal node.

Table 4.1 Logistic regression model parameters for predicting presence/absence of WPBR

Parameter	DF	Estimate	S.E.[1]	p[2]	95% C.I.	
Intercept	1	-73.525	9.394	<0.0001	-93.55	-56.54
May Relative Humidity	1	0.643	0.097	<0.0001	0.466	0.851
September Relative Humidity	1	0.446	0.117	0.0001	0.234	0.696
May-June Mean Max. Temp. (°C)	1	-1.413	0.400	0.0004	-2.213	-0.634
July-August-September Mean Max. Temp. (°C)	1	1.855	0.462	<0.0001	0.967	2.794
Stream Density (km stream/km^2)	1	35.447	11.995	0.003	12.462	59.808
Stream Density * September Relative Humidity	1	-0.678	0.235	0.004	-1.155	-0.226

[1] Standard error of parameter estimate
[2] P-value based on Wald Chi-Square statistic

Table 4.2. Estimated probability of presence of white pine blister rust in 16 study areas in central and southeastern Wyoming and Colorado.

		Predicted Probability			Proportion
Site	**N[1]**	**Mean**	**S. D.[2]**	**Range**	**Infested[3]**
Ferris Mountain	7	0.896	0.082	0.760-0.963	0.571
Green Mountain	22	0.955	0.033	0.878-0.994	1.000
Horse Creek, SNF	20	0.873	0.086	0.718-0.992	0.950
Laramie Peak East	29	0.956	0.040	0.837-0.992	0.966
Laramie Peak West	30	0.722	0.268	0.169-0.997	0.600
Muddy Mountain	20	0.825	0.110	0.678-0.992	0.950
Northern Snowy	60	0.209	0.190	0.012-0.640	0.217
Pole Mountain	93	0.924	0.051	0.751-0.992	0.914
Roosevelt NF - survey	75	0.456	0.249	0.068-0.871	0.267
Roosevelt NF - other	44	0.353	0.235	0.022-0.808	0.091
San Isabel NF	15	0.221	0.285	0.001-0.814	0.333
Sangre de Cristo	30	0.084	0.103	0.001-0.407	0.467
Shirley Mountains	33	0.901	0.070	0.739-0.990	0.909
Southern Snowy	69	0.248	0.168	0.028-0.770	0.072
Wet Mountains	50	0.379	0.305	0.023-0.948	0.220
Wind River	15	0.945	0.087	0.670-0.995	1.000

[1] Number of survey plots established within study area. Plots in the Roosevelt N.F., San Isabel N.F. Sangre de Cristo, and Wet Mountains site were established by other crews using similar methods. All other plots were established by this author and her field crews.
[2] Standard deviation of the mean.
[3] Based on survey plots.

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Table 4.3 Regression models for predicting disease pressure.

Model 1										
Parameter	**DF**	**Estimate**	**S.E.[1]**	**p[2]**	**95% C.I.[3]**		**R^2**	**Cp[4]**	**AIC[5]**	**PRESS[6]**
Intercept	1	-6.257	1.020	<0.0001	-8.261	-4.253	0.792	7.00	186.28	323.96
Years	1	0.279	0.009	<0.0001	0.262	0.296				
September Precipitation (mm)	1	0.037	0.010	0.0001	0.018	0.056				
June Max. Temp. (°C)	1	-0.397	0.131	0.0025	-0.654	-0.141				
July Max. Temp. (°C)	1	0.046	0.130	0.0004	0.205	0.715				
August Relative Humidity	1	-0.109	0.025	<0.0001	-0.157	-0.060				
September Relative Humidity	1	0.156	0.027	<0.0001	0.103	0.209				

Model 2										
Parameter	**DF**	**Estimate**	**S.E.[1]**	**p[2]**	**95% C.I.[3]**		**R^2**	**Cp[4]**	**AIC[5]**	**PRESS[6]**
Intercept	1	-7.706	1.584	<0.0001	-10.819	-4.593	0.789	7.00	181.51	326.69
Years	1	0.282	0.009	<0.0001	0.265	0.299				
September Precipitation (mm)	1	0.043	0.010	<0.0001	0.025	0.062				
August Relative Humidity	1	-0.121	0.024	<0.0001	-0.169	-0.074				
September Relative Humidity	1	0.139	0.032	<0.0001	0.075	0.203				
June Relative Humidity	1	0.076	0.034	0.0238	-0.169	-0.074				
July-August-September Mean Max. Temp. (°C)	1	0.086	0.038	0.0258	0.010	0.161				

Disease pressure measured in terms of canker bins occupied (15.24 cm canker size classes).
[1] Standard error of the estimate, [2] P-value based on t-test, [3] 95% confidence interval for estimate, [4] Mallow's Cp, [5] Akaike Information Criterion, [6] predicted residual sum of squares.

Table 4.4. Pearson's correlation coefficients[1] between climate variables and white pine blister rust disease pressure represented as occupied canker bins, incidence, and relative severity index (RSI) based on 473 survey plots used to develop regression models.

	Disease Pressure[2]	Incidence[3]	Relative Severity Index[4]
May precipitation (mm)	0.324 ****	0.361 ****	0.342 ****
June precipitation (mm)	0.404 ****	0.392 ****	0.391 ****
July precipitation (mm)	0.120 **	0.080 n.s.	0.110 *
August precipitation (mm)	0.264 ****	0.200 ****	0.216 ****
September precipitation (mm)	0.000 n.s.	-0.035 n.s.	-0.016 n.s.
May min. temp. (°C)	0.427 ****	0.509 ****	0.465 ****
June min. temp. (°C)	0.437 ****	0.522 ****	0.480 ****
July min. temp. (°C)	0.460 ****	0.544 ****	0.505 ****
August min. temp. (°C)	0.459 ****	0.557 ****	0.513 ****
September min. temp. (°C)	0.448 ****	0.551 ****	0.508 ****
May max. temp. (°C)	0.211 ****	0.177 ****	0.179 ****
June max. temp. (°C)	0.214 ****	0.176 ****	0.188 ****
July max. temp. (°C)	0.309 ****	0.282 ****	0.286 ****
August max. temp. (°C)	0.328 ****	0.337 ****	0.331 ****
September max. temp. (°C)	0.232 ****	0.204 ****	0.213 ****
May relative humidity	0.470 ****	0.512 ****	0.477 ****
June relative humidity	0.404 ****	0.505 ****	0.470 ****
July relative humidity	-0.026 n.s.	-0.074 n.s.	-0.030 n.s.
August relative humidity	-0.021 n.s.	-0.091 *	-0.051 n.s.
September relative humidity	0.274 ****	0.259 ****	0.273 ****
May/June mean min. temp. (°C)	0.434 ****	0.518 ****	0.475 ****
July/August/Sept. mean min. temp. (°C)	0.459 ****	0.554 ****	0.512 ****
May/June mean max. temp. (°C)	0.214 ****	0.178 ****	0.185 ****
July/August/Sept. mean max. temp. (°C)	0.298 ****	0.283 ****	0.285 ****
May/June mean precipitation (mm)	0.391 ****	0.410 ****	0.397 ****
July/August/Sept. mean precipitation (mm)	0.157 ***	0.102 *	0.128 **

[1] significance levels: 0.0001=****, 0.001=***, 0.01=**, *=0.05, ns=p>0.05.
[2] Disease pressure = number of occupied 15.24 cm canker bins.
[3] Incidence = proportion of infected trees.
[4] Relative severity index = measure of expected biological impact based on affected tree size and number and location of cankers.

Table 4.5 Regression models for predicting white pine blister rust incidence.

Model 1										
Parameter	**DF**	**Estimate**	**S.E.[1]**	**p[2]**	**95% C.I.[3]**		**R^2**	**Cp[4]**	**AIC[5]**	**PRESS[6]**
Intercept	1	-1.445	0.269	<0.0001	-1.972	-0.917	0.631	10.00	1896.75	8.68
Years	1	0.016	0.001	<0.0001	0.014	0.019				
Proportion DBH > 15.5 cm	1	0.002	0.000	<0.0001	0.001	0.003				
Log_{10} *Ribes inerme* density w/in 1 km	1	0.017	0.004	<0.0001	0.009	0.024				
September Min. Temp. (°C)	1	-0.487	0.121	<0.0001	-0.723	-0.250				
June Relative Humidity	1	0.029	0.005	<0.0001	0.019	0.040				
Mean May/June Precipitation (mm)	1	-0.002	0.001	0.1407	-0.004	0.001				
Mean May/June Min. Temp. (°C)	1	0.425	0.115	0.0002	0.199	0.652				
September Min. Temp. * Mean May/June Precip.	1	0.010	0.002	<0.0001	0.006	0.013				
Mean May/June Precip * Mean May/June Min. Temp.	1	-0.008	0.002	<0.0001	-0.012	-0.004				

Model 2										
Parameter	**DF**	**Estimate**	**S.E.[1]**	**p[2]**	**95% C.I.[3]**		**R^2**	**Cp[4]**	**AIC[5]**	**PRESS[6]**
Intercept	1	-1.895	0.237	<0.0001	-2.360	-1.430	0.662	7.00	1943.61	7.83
Canker bins	1	0.065	0.004	<0.0001	0.058	0.073				
Proportion DBH > 15.5 cm	1	0.002	0.000	0.0001	0.001	0.003				
Bottom Slope	1	0.033	0.016	0.0366	0.002	0.065				
Mean May/June Min. Temp. (°C)	1	-0.062	0.019	0.0009	-0.099	-0.026				
Mean July/August/September Min. Temp. (°C)	1	0.075	0.016	<0.0001	0.043	0.107				
June Relative Humidity	1	0.033	0.005	<0.0001	0.023	0.042				

[1] Standard error of the estimate, [2] P-value based on t-test, [3] 95% confidence interval for estimate, [4] Mallow's Cp, [5] Akaike Information Criterion, [6] predicted residual sum of squares.

Table 4.6. Mean white pine blister rust relative severity index on 13 study areas in central and southeastern Wyoming and northern Colorado.

Site	N[1]	Relative Severity Index[2]
Wind River	15	2.69 a
Green Mountain	22	1.69 b
Muddy Mountain	20	1.66 b
Pole Mountain	93	1.58 bc
Laramie Peak East	29	1.51 bc
Ferris Mountain	7	1.26 bc
Shirley Mountains	33	1.05 bcd
Horse Creek, SNF	20	0.79 cde
Laramie Peak West	30	0.30 de
Roosevelt NF	75	0.18 e
Northern Snowy	60	0.05 e
Southern Snowy	69	0.05 e
Sierra Madre	31	0.00 e

[1] N = the number of plots established within each study site.
[2] Mean relative severity index, means followed by different letters are significantly different at p=0.05 based on Tukey's HSD.

Appendix 4.1. Pearson's correlation coefficients[1] of PRISM temperature minimums and maximums (°C) for 504 surveyed plots in southeastern and central Wyoming and northern Colorado

	May T. min.	June T. min.	July T. min.	August T. min.	September T. min.	May T. max.	June T. max.	July T. max.	August T. max.	September T. max.
May T. min.		0.987**	0.961**	0.965**	0.962**	0.639**	0.569**	0.649**	0.745**	0.541**
June T. min.	0.987**		0.990**	0.987**	0.979**	0.602**	0.550**	0.644**	0.736**	0.522**
July T. min.	0.961**	0.990**		0.987**	0.975**	0.581**	0.542**	0.646**	0.724**	0.520**
August T. min.	0.965**	0.987**	0.987**		0.984**	0.499**	0.454**	0.567**	0.677**	0.438**
September T. min.	0.962**	0.979**	0.975**	0.984**		0.528**	0.491**	0.584**	0.685**	0.478**
May T. max.	0.639**	0.602**	0.581**	0.499**	0.528**		0.968**	0.930**	0.874**	0.933**
June T. max.	0.569**	0.550**	0.542**	0.454**	0.491**	0.968**		0.966**	0.903**	0.967**
July T. max.	0.649**	0.644**	0.646**	0.567**	0.584**	0.930**	0.966**		0.955**	0.959**
August T. max.	0.745**	0.736**	0.724**	0.677**	0.685**	0.874**	0.903**	0.955**		0.918**
September T. max.	0.541**	0.522**	0.520**	0.438**	0.478**	0.933**	0.967**	0.959**	0.918**	

[1]** significant at p=0.001, * significant at p=0.05.

Appendix 4.2. Variables used to create classification trees to predict the presence and absence of white pine blister rust on 10 study areas in central and southeastern Wyoming

Variable Name	Type	Description
WPBR		Response variable. 0=no rust, 1=rust
slope_pct	Plot	percent slope measure with an inclinometer
aspect	Plot	SW (135-314°) and NE (315-360° and 1-134°)
pos	Plot	slope position: bottom, mid-slope, shoulder, and summit/ridge
stand	Plot	open canopy, closed canopy, mosaic of open and closed
PIPO	Plot	presence/absence of ponderosa pine
PICO	Plot	presence/absence of lodgepole pine
ABLA	Plot	presence/absence of subalpine fir
mExt_inerme_mha	Plot	mean density of *Ribes inerme* (m/ha) in extensive survey plots within 1km radius of plot
dc_1	Plot	proportion of trees in plot <5.1cm DBH
dc_2	Plot	proportion of trees in plot 5.1 - 15.25 cm DBH
dc_34	Plot	proportion of trees in plot >15.25 cm DBH
cc_cd	Plot	proportion of trees in plot in dominant and codominant crown classes
cc_in	Plot	proportion of trees in plot in intermediate crown class
cc_op	Plot	proportion of trees in plot in open crown class
cc_ovun	Plot	proportion of trees in plot in overtopped and understory crown classes
percent live crown	Plot	mean percent live crown
tph2	Plot	density of limber pine in trees per hectare
streamdist_100k	Plot	distance to nearest stream, 1:100000 scale GIS layer from USGS's National Hydrography Dataset
streamdist_24k	Plot	distance to nearest stream, 1:24000 scale GIS layer from USDA Forest Service
streamdens_100k	Plot	density of streams within 1 km radius of plot, 1:100000 from USGS's National Hydrography Dataset
streamdens_24k	Plot	density of streams within 1 km radius of plot, 1:24000 scale GIS layer from USDA Forest Serivce

Appendix 4.2 continued.

Variable Name	Type	Description
may_ppt		PRISM 30 yr average of May precipitation (mm)
june_ppt		PRISM 30 yr average of June precipitation (mm)
july_ppt		PRISM 30 yr average of July precipitation (mm)
august_ppt		PRISM 30 yr average of August precipitation (mm)
sep_ppt		PRISM 30 yr average of September precipitation (mm)
may_tmin		PRISM 30 yr average minimum temperature in May (°C)
june_tmin		PRISM 30 yr average minimum temperature in June (°C)
mj_tmin		PRISM mean of may_tmin and june_tmin (°C)
july_tmin		PRISM 30 yr average minimum temperature in July (°C)
august_tmin		PRISM 30 yr average minimum temperature in August (°C)
sep_tmin		PRISM 30 yr average minimum temperature in September (°C)
jas_tmin		PRISM mean of july_tmin, august_tmin, and sep_tmin (°C)
may_tmax		PRISM 30 yr average maximum temperature in May (°C)
june_tmax		PRISM 30 yr average maximum temperature in June (°C)
mj_tmax		PRISM mean of may_tmax and june_tmax (°C)
july_tmax		PRISM 30 yr average maximum temperature in July (°C)
august_tmax		PRISM 30 yr average maximum temperature in August (°C)
sep_tmax		PRISM 30 yr average maximum temperature in September (°C)
jas_tmax		PRISM mean of july_tmax, august_tmax, and sep_tmax (°C)
RH_05		PRISM 30 yr average of May relative humidity
RH_06		PRISM 30 yr average of June relative humidity
RH_07		PRISM 30 yr average of July relative humidity
RH_08		PRISM 30 yr average of August relative humidity
RH_09		PRISM 30 yr average of September relative humidity
FF_Med		PRISM 30 yr median length of frost-free period

Appendix 4.3. Rust Severity index

This rust severity index (RSI) was modified from one developed by Duriscoe and Duriscoe (2002). This index is intended to reflect the biological impact of WPBR infection, with higher RSI values reflecting higher probability of significant impact to the host, rather than just a count of branch and stem cankers per tree. Values for the RSI ranged from 0 to 10 and were calculated, as shown below, for each tree evaluated. Individual tree RSIs were then averaged for the plot to provide a plot-level RSI.

RSI = RIC + RID

Where **RIC** = 0 for no cankers
1 for 1 – 5 branch cankers and 0 stem cankers
2 for 6 – 10 branch cankers and 0 stem cankers
3 for 11 – 25 branch cankers and 0 stem cankers
4 for > 25 branch cankers and 0 stem cankers
5 for 1 stem cankers, regardless of the number of branch cankers
6 for > 1 stem cankers, regardless of the number of branch cankers

RID = 0 when RIC=0, and when RIC>0
1 when diameter at breast height (DBH) > 30.5 cm
2 when DBH 15.5 – 30.5 cm
3 when DBH 5.1 – 15.4 cm
4 when DBH < 5.1 cm

For example, a 5 cm DBH limber pine with 1 stem canker would have an RSI of 9 (5+4), while a 50 cm DBH limber pine with 20 branch cankers would have a RSI of 4 (3+1) indicating a higher likelihood of significant damage to the first tree.