THESIS

LIMBER PINE HEALTH IN THE SOUTHERN AND CENTRAL ROCKY MOUNTAINS

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ABSTRACT

LIMBER PINE HEALTH IN THE SOUTHERN AND CENTRAL ROCKY MOUNTAINS

White pine blister rust, bark beetles, and dwarf mistletoe are causing decline in health and mortality in limber pine and impacting limber pine seedlings in the central and southern Rocky Mountains. Ecologically valuable limber pines often grow in fragile ecosystems where few other trees can grow. The combined effects of mountain pine beetle, white pine blister rust, dwarf mistletoe, and climate change could greatly impact the biodiversity of these ecosystems. Current condition status and long term monitoring of limber pine trees and seedlings are needed to advise land managers and to implement restoration. Our study objectives were to: (1) assess site, stand, and health characteristics of limber pine trees and seedlings in Colorado, Wyoming, and Montana, (2) determine factors that influence the occurrence and incidence of white pine blister rust, bark beetles, and dwarf mistletoe, and (3) determine factors that impact seedlings, including site, stand, and meteorological characteristics.

In 2011 and 2012, we assessed 22,700 limber pines on 508 plots in limber pine-dominated stands in twenty-five study areas in Colorado, Wyoming, and Montana. Mean density of live limber pine was 311 stems/ha. Fifty percent of all standing trees were classified as healthy, 26% were declining or dying, and 24% were dead. White pine blister rust was the primary damage agent and was widespread, occurring in 23 of the 25 study areas with a mean incidence of 26%. Bark beetle-caused mortality occurred in all 25 study areas and 18% of standing limber pines were killed by bark beetles. Limber pine dwarf mistletoe occurred within 20 study areas, on 29% of plots with an average incidence of 9%. In previously monitored study areas, incidence of WPBR increased 6%, bark beetles by 17%, while dwarf mistletoe remained the same. Live limber pine seedling density averaged 141stems/ha. Of all standing live and dead limber pine seedlings, 1.5% were dying, 4.4% were dead, and white pine blister rust occurred on 5.3% of live seedlings.

We used statistical modeling to determine the meteorological, macro, and micro site factors and stand factors that influenced the occurrence and incidence of white pine blister rust, bark beetles, and dwarf mistletoe on limber pines. We also used statistical modeling to determine factors that predict density (stems/ha) of limber pine seedlings and proportion of limber pine seedlings with white pine blister rust. Limber pine stands heavily impacted by mountain pine beetle and white pine blister rust, combined with low seedling density in some study areas suggest that some limber pine stands may not survive. These areas may be in need of additional monitoring so land managers can decide if restoration efforts are warranted.

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1. Introduction

Limber pines (*Pinus flexilis* James) are ecologically valuable five-needle white pines with a widespread distribution. Recent studies have indicated the growing impact white pine blister rust (WPBR), which is caused by the introduced fungal pathogen, *Cronartium ribicola* J. C. Fisch. Major, has had on white pine populations (Kearns and Jacobi 2007, Maloney 2011, Smith et al. 2008, Smith et al. 2013). Other major disturbance agents that cause dieback and mortality in limber pine are limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* [A. Nelson ex Rydb.]) and bark beetles, including the more recent outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Kearns and Jacobi 2007, Taylor and Mathiason 1999). Little is known about how these disturbance agents will impact limber pines. Understanding abiotic and biotic factors that influence the occurrence and incidence of WPBR, bark beetles, and dwarf mistletoe, will be helpful in determining appropriate management actions to sustain limber pine populations.

Limber pines are broadly distributed in western North America, occurring between 34 and 54 degrees latitude and between 870 and 3810 m in elevation (Steele 1990). In the central Rocky Mountains, limber pines are found from lower to upper tree line, occur between a larger elevation range (1600 and 3400 m) than other 5-needle pines (Schoettle and Rochelle 2000), and are frequently found in association with Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), quaking aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* Douglas ex Loudon), Douglas-fir (*Pseudotsuga* *menziesii* [Mirb.] Franco), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), and occasionally whitebark pine (*Pinus albicaulis* Engelm.) (Peet 1981, Steele 1990). Limber pines are a shade-intolerant species that occur in scattered, low-density stands and often grow on rocky, xeric sites where cold temperatures, short growing seasons, and soil characteristics limit the growth of other conifer species (Schoettle and Rochelle 2000, Schoettle 2004). At lower elevations on mesic sites with deep soils, other conifer species are more competitive and white pines are often considered a seral component (Kendall and Arno 1990, Arno and Weaver 1990).

Limber pines are revered for their cultural, recreational, and aesthetic value, and are beneficial components of forest ecosystems. Limber pines often define tree lines, stabilize soil and snowpack, provides facilitative mechanisms such as shade and wind reduction for understory species (Baumeister and Callaway 2006), aid in the establishment of late successional species, are one of the first tree species to occupy an area after fire (Donnegan and Rebertus 1999), and provide a habitat and food source for animals (Schoettle 2004). Limber pine seeds are wingless and rely on Clark's nutcracker (*Nucifraga columbiana* Wilson) and pinyon jays (*Gymnorhinus cyanocephalus* Wied) for long-distance dispersal. Clark's nutcracker can cache seeds distances greater than 22 kilometers from the source (Lorenz et al. 2011) and often do so in burn areas (Lanner and Vander Wall 1980).

Cronartium ribicola, the pathogen that causes WPBR, is native to Asia but has been present in North America since 1910, when it was introduced on nursery stock from Europe. *Cronartium ribicola* is a heteroecious rust capable of infecting all North American white pines (five-needled pines) and must use *Ribes* species (currants and gooseberries), *Pedicularus* species, or *Castilleja* species as alternate hosts to complete a complex life cycle requiring five spore stages (McDonald et al. 2006). Infection of pines occurs through needles, during periods of high relative humidity in late summer and fall. The fungus then grows into the branch, causing swelling and ultimately, a canker that may girdle the branch and continue expanding into the main stem in which topkill or tree death may occur. Aeciospores, the durable spores produced on the white pine, are able to travel on wind currents up to several hundred kilometers to infect leaves of the alternate hosts (Frank et al. 2008). Basidiospores, the fragile spores produced on the leaves of alternate hosts in late summer to fall, are wind disseminated, traveling up to 27 kilometers to white pines (Zambino 2010). Infection can lead to loss of vigor, a reduction in seed production, death of cone-bearing branches (Maloney et al. 2012), and ultimately mortality, which can occur several years after infection with time depending on the size of the tree. Seedlings are also susceptible and can die within three years of infection (Hoff and Hagle 1990).

Since its introduction into western North America in southern British Columbia, WPBR has spread south and east in the Rocky Mountains during the last century. From its discovery in Montana in 1928 (Putnam 1931), it has moved from western Wyoming (Krebill 1964, Brown 1970) to southeastern Wyoming (Brown 1978), and was reported in Colorado in 1998 with highest infection south of the Wyoming border (Johnson and Jacobi 2000). In addition, WPBR was first reported on Rocky Mountain bristlecone pine in the Great Sand Dunes National Monument in Colorado in 2003 (Blodgett and Sullivan 2004). Previous assessments in 2002-2004 in the southern and central Rocky Mountains indicated that 55% of surveyed plots were infected with WPBR, with a mean overall incidence of 16% (Kearns and Jacobi 2007). There is concern that most limber pine populations may be at risk of infection as the pathogen continues to spread throughout the Rocky Mountain region (Johnson and Jacobi 2000).

Until the recent mountain pine beetle epidemic, limber pine dwarf mistletoe was considered the second most damaging agent of limber pine behind WPBR (Taylor and Mathiason 1999). *Arceuthobium cyanocarpum* is an especially virulent dwarf mistletoe and known to cause widespread mortality of limber pine in the Rocky Mountains (Mathiasen and Hawksworth 1988). Limber pine dwarf mistletoe occurs in California, Oregon, Idaho, Nevada, and Utah, and is widely distributed in the Rocky Mountains from southern Colorado, throughout Wyoming, and up to southern Montana, and ranges in elevation from 1,600 to 3,050 m (Geils et al. 2002). Dwarf mistletoe is disseminated short distances by using hydrostatic pressure to forcefully eject sticky seeds to surrounding branches. Birds known to eat the seeds of *A.cyanocarpum*, such as Mountain Bluebirds (*Sialia currucoides* Bechstein) and mourning doves (*Zenaida macroura* Linnaeus) and birds and mammals that frequent limber pine stands, disperse the seeds long distances (Hawksworth and Wiens 1996, Geils et al. 2002).

Mountain pine beetle has caused extensive mortality throughout the central Rocky Mountain region. From 1996 to 2013, 2.75 million hectares in Colorado and Wyoming have been affected by mountain pine beetle, with peak years occurring in 2008 and 2009 (USDA Forest Service, Aerial Detection Survey 2013). The northern Medicine Bow Mountains experienced the highest mortality and northern Wyoming forests were heavily impacted. Recent aerial survey reports indicate that while some areas are continuing to spread, overall, mountain pine beetle-caused mortality has declined dramatically, primarily due to host depletion (USDA Forest Service, Aerial Detection Survey 2013).

Mountain pine beetle, the most immediate threat as compared to WPBR or dwarf mistletoe, prefers larger diameter trees (Safranyik and Carroll 2006) and can result in rapid and widespread mortality of cone-bearing trees important to regeneration during epidemic levels.

Smaller diameter trees and seedlings unaffected by mountain pine beetle are still at risk of mortality from WPBR and dwarf mistletoe. White pine blister rust (Keane and Arno 1993, Bockino and Tinker 2012) and drought may each predispose the tree to increased susceptibility to mortality by the mountain pine beetle (Six and Adams 2007). It is of primary concern that the mountain pine beetle may be attacking WPBR resistant trees. Mountain pine beetle, along with the added impacts of WPBR, which continues to spread and intensify in limber pine (Burns et al. 2006, Kearns and Jacobi 2007, Smith and Hoffman 2001), could be devastating to some limber pine populations.

Recent mortality of limber pine due to WPBR, dwarf mistletoe, and bark beetles requires better understanding of the characteristics that influence these major disturbance agents so land managers may employ effective management decisions to encourage sustainment of limber pine populations. Previous work has shown various site, stand, and meteorological characteristics to impact WPBR, dwarf mistletoe, and bark beetles, but very few studies have looked at what impacts these disturbance agents in limber pine, and no studies have addressed all three in limber pine. In addition to suitable host and inoculum source, other studies have shown that the distribution of WPBR is influenced by site, stand, and meteorological characteristics (Campbell and Antos 2000, Smith and Hoffman 2001, Duriscoe and Duriscoe 2002, Kearns and Jacobi 2007, Larson 2010, Kearns et al. 2013). While the primary factors impacting the occurrence and incidence of dwarf mistletoe include an inoculum source, suitable hosts within appropriate distance for natural dispersal, and availability and activity of avian vectors, secondary factors, including site, stand, and meteorological characteristics may be important in determining the distribution of dwarf mistletoe (Hawksworth and Wiens 1996, Taylor and Mathiason 1999).

While distribution and incidence of bark beetles is largely influenced by beetle pressure, some stand, and meteorological characteristics have been found to influence bark beetles (Carroll et al. 2003, Larson 2010).

While some prior knowledge exists of the extent of impact of WPBR and limber pine dwarf mistletoe in the southern and central Rocky Mountains, recent impact by mountain pine beetle in limber pine is largely unknown. The objectives of this study were to (*i*) assess site, stand, and health characteristics of limber pine stands northern Colorado, Wyoming, and Montana and (*ii*) determine factors that influence the incidence of white pine blister rust, dwarf mistletoe, and mountain pine beetle in limber pine, including site, stand, and meteorological characteristics.

2. Materials and Methods

Site, stand, and health assessments of limber pine stands included measuring the size and determining the status of all trees, standing dead or alive within fixed area plots. Trees were examined for damages including, occurrence and severity of white pine blister rust, bark beetles, dwarf mistletoe, and any other additional damages. Site and stand features were noted along with the amount and type of groundcover, and occurrence of alternate hosts of WPBR. White pine blister rust, dwarf mistletoe, and bark beetle occurrence and incidence on limber pine were modeled to determine the influence of environmental factors and stand structure on each damage agent.

2.1. Study areas

The geographic range of our monitoring study included the eastern-most mountain range of the Rocky Mountains in northern Colorado (Front Range) and in Wyoming we included the eastern mountain ranges (Medicine Bow, Laramie, and Bighorn Mountains) and next mountain ranges of the Rocky Mountains to the west (Sierra Madre, Wind River Range, Absaroka Range) with all minor mountains and basins in between and one mountain range in southern Montana (Pryor Mountains) and another in eastern Montana (Terry Badlands) (Figure 1.1). We conducted surveys on twenty-five study areas in these geographic areas that were defined by government management unit boundaries and geographic sections of mountain ranges (Table 1.1, Figure 1.1).

2.2. Stand selection

2.2.1. Stands previously sampled

Potential plot locations in each study area were identified using USDA Forest Service Aerial Detection Survey data on areas with mountain pine beetle-caused mortality in limber pine and GPS location data from previous sampling and monitoring efforts by Kearns and Jacobi (2007) and Burns et al. (2011). Using the USDA Forest Service Rocky Mountain Resource Inventory System database to determine the presence of limber pine, Kearns and Jacobi (2007) poststratified to capture varying site conditions and sampled limber pine across an elevational gradient that reflected that of the study area. We used a random stratified sample of these locations so there was relatively equal number of plots with low and high rust infestation and presence or absence of bark beetle outbreak. A range of stands were sampled with varying duration since bark beetle outbreak. Where possible, a minimum of 24 plots per study area were installed to account for low and high WPBR infestation levels and presence or absence of bark beetle-caused mortality with six plots of each. If an insufficient number of stands were found for a particular category, then remaining plots were selected to fill the other stratification variables equally. Plot locations were within 300 meters of a road. The number of plots within a study area varied depending on the amount of the area with limber pine, previous knowledge of the variation in WPBR incidence and severity, aerial detection data on MPB incidence, and accessibility.

2.2.2. Stands not previously sampled

Potential plot locations were selected in each study area where no prior surveys were conducted for WPBR. The areas were based on known records of host location, aerial detection information on mountain pine beetle-caused mortality, and local knowledge of host location. A stratified random sample of these locations was conducted so there were relatively equal numbers of plots below and above the mid elevation of the limber pine distribution in the study area and presence or absence of bark beetle-caused mortality. Where possible, a minimum of 24 plots per study area were installed to account for two elevation ranges and bark beetle infestation and six plots of each. Remaining protocol followed that of the stands previously sampled.

2.3. Survey methods

2.3.1. Plot establishment

To ensure a reasonable sample of limber pine in our monitoring study, plots were placed in stands with at least 40% adult limber pine (stems/ha). Plots were randomly located on a compass bearing that placed the plot within the limber pine stand and at least 10 m from a road. A plot consisted of three 60 x 6 m fixed area subplots (0.108 ha) that were used for tree assessments with an invasive species/alternate host plot (30 x 6 m) placed after each 60 x 6 m subplot (0.054 ha) and were placed contiguously at random bearings within the stand. Individual trees were not tagged, but one tree was tagged and marked with GPS at the beginning of each subplot and the end of the third subplot. Within each 60 x 6 m subplot, the following site data were recorded: elevation (m), aspect (degrees), slope percent, slope position (position on the landscape: backslope = steepest inclined surface, footslope/toeslope/valley bottom = inner, gentle inclined surface at base of hillslope/gentle inclined surface at base of hillslope/wide valley bottom beyond toeslope, shoulder = uppermost inclined surface near the top of a hillslope, summit = highest level of hillslope position) (USDA Soil Conservation Service), stand structure (distribution of tree height classes within a stand: closed canopy multistory, closed canopy multistory with open individuals and/or open scattered clumps, closed canopy single story with open individuals and/or open scattered clumps [includes mosaic of closed canopy single and multistory], open canopy scattered individuals and/or open canopy scattered clumps), and disturbance history (fire, grazing, other human disturbance, tree cutting).

2.3.2. Trees

Within each subplot, the following data were recorded for all tree species, standing dead and alive with a dbh (diameter at breast height) at 1.37 m (no minimum diameter): species, crown class (description of the relative position of the tree crown with respect to competing vegetation near the tree: dominant/co-dominant = crown receives full light from above and partly from the sides/crown receives full light from above but little on the sides, intermediate = crown occupies a subordinate position and is subject to strong lateral competition, open = crown receives full light from above and all sides, overtopped/understory = crown receives no direct light from above), dbh to nearest cm using a Biltmore stick for efficiency, 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 [0-5 years] = no green needles but some red needles and fine twigs present, old dead [5-10 years] = no fine twigs or needles present, >50% bark still present, very old dead [>10 years] = no fine twigs, no needles, <50% bark present), percent crown dieback (percentage of dead foliage as compared to the entire crown), dwarf mistletoe rating (DMR) (Hawksworth 1977), bark beetle presence (none, unsuccessful MPB bole attack: pitchout and beetle brood absent, MPB strip attack: galleries and brood present, successful MPB bole attack, unknown or other bark beetle). Within each subplot, the following data were recorded for all limber pine, standing dead and alive with a dbh at 1.37 m (no minimum diameter): WPBR canker presence and location (branch, stem, both), total number of WPBR branch and stem cankers, branch canker length by 12 cm size classes on live trees of the first ten representative cankers on live branches, as an estimate of canker age (<12 cm, 12-24 cm, 24.1-36 cm, 36.1-48 cm, 48.1-60 cm, 60.1-72 cm, 72.1-84 cm, 84.1-96 cm, 96.1-108 cm, =>108.1 cm) and status of branch tip with canker for each of the first ten representative cankers (alive or dead), and type and severity of up to two damages affecting 5% or more of the tree. Cankers were identified as such if two of the following were present: abnormal swollen branch, blistered branch or stem, aecia present, roughened resin stained bark, or expanding areas of squirrel bark removal. Cankers were defined as stem cankers if they were located on the main stem or were within 15 cm of the stem on living branches. Since mature limber pine have multiple leaders, a stem was defined that if girdled would remove more than 25% of the crown. Binoculars were used to identify cankers in taller trees. Trees growing in clumps were considered individual stems if they forked below 1.37 m height and were growing at an angle greater than 45° above horizontal.

2.3.3. Ground cover

Two circular fixed area subplots with a 3 m radius were placed 3 m from each end within the 60 x 6 m subplots to record ground cover and understory vegetation. Within each circular subplot, the following data were recorded: percent of area occupied by each ground cover type (soil, litter, rock, tree/log, lichen/moss, grass/sedges, forbs, shrubs) and up to three of the most prevalent shrub species and percent of area occupied by each of those species. All field crew members' ocular estimates were calibrated to a single, consistent estimation.

2.3.4. White pine blister rust alternate hosts

At the end of each 60 x 6 m subplot, along the same bearing, an alternate host plot (30 x 6 m) was established in which the presence and ground area occupied (cm^2) by alternate hosts of WPBR, including *Ribes, Castilleja*, and *Pedicularis* species were recorded. Presence and ground area occupied by *Ribes* species were recorded in previously non-monitored plots and these data were obtained from the original survey on previously monitored plots.

2.4. Meteorological data

Factors that may influence WPBR, dwarf mistletoe, and bark beetles, that could not be collected in the field included meteorological data obtained from the PRISM dataset (Daly et al. 2002) provided by FHTET (USDA FS Forest Health Technology Enterprise Team, Fort Collins, CO). For each plot, meteorological data included 30-year (1981-2010) monthly averages on a 1-km resolution grid for daily minimum and maximum temperatures (°C), precipitation (mm), relative humidity (%), and additional meteorological variables such as drought frequency, growing degree days, and seasonal moisture index, totaling 133 variables (Appendix I, Table 1.13). We also screened each daily temperature range, precipitation, and relative humidity averaged for the individual months from May to September and for the two periods of May–June and July–September.

Additional monthly and yearly meteorological data was extracted from Daymet Daily Surface Gridded Data (Thornton et al. 2012). Daymet only provides daily water vapor pressure ambient values (VP_{amb}), so relative humidity calculations were produce using calculations from Zimmermann and Roberts (2001). For each plot, extracted meteorological data included monthly and yearly averages on a 1-km resolution grid from 2000-2012 for minimum and maximum temperatures (°C) and relative humidity (%) and monthly and yearly totals for precipitation (mm) and totaled 270 variables (Appendix I, Table 1.14).

GIS layers with stream distributions from the USGS National Hydrological High Definition Dataset (available at http://nhd.usgs.gov/) were used to estimate the density of perennial and intermittent streams within a 1-km radius of each survey plot (km/km2). Stream density was used as a surrogate measure for the location of *Ribes* species that occupy moist or riparian sites.

2.5. Data analyses

Data transformations were carried out on certain mature tree data prior to any analysis. Stem density was calculated on the basis of the area of the three subplots established. WPBR disease, bark beetle, and dwarf mistletoe incidence was calculated as the number of infected trees/number of evaluated trees. Mean WPBR severity was calculated as the average number of cankers per infected pine. Species other than limber pine and aspen were combined into general groups: other pines included lodgepole, ponderosa, and whitebark pine, spruce-fir included Douglas-fir, subalpine fir, Engelmann spruce, and white spruce [*Picea glauca* (Moench) Voss], and other species included Rocky Mountain and Utah juniper [*Juniperus osteosperma* (Torr.) Little]. Stem density (stems/ha) and basal area were transformed to a $\log_{10}$ scale and percent stems with WPBR, bark beetles, and dwarf mistletoe and percent cover of *Ribes inerme* Rydb. were square root transformed to normalize skewed data.

All data analyses were performed using SAS software, Version 9.3 of the SAS System for Windows, Copyright © [2002-2010] SAS Institute Inc. SAS and all other SAS Institute Inc., Cary, NC, USA. Simple descriptive statistics were produced for DBH, density (stems/ha), basal area (m²/ha), health status, and allocation of damage to declining or dying and dead limber pine and are presented in Table 1.1, Figure 1.2, and 1.3. Least square means were produced using PROC GLIMMIX (with /s dist=binary) for occurrence and PROC MIXED for incidence of WPBR, bark beetles, and dwarf mistletoe, and are presented in Figure 1.4 and1. 5. Overall means and means by study area were determined using plot-level means, unless otherwise noted.

Using the subplot-level variables (Appendix I, Tables 1.11-1.14), logistic regression was used to determine which variables can predict occurrence of each WPBR, bark beetles, and dwarf mistletoe, and linear regression was used to determine the variables that predict percent of stems with each of the three main damage agents. Stem density (stems/ha) and basal area (m²/ha) variables were transformed to a $\log_{10}$ scale to normalize skewed data. Percent stems with WPBR, bark beetles, dwarf mistletoe, and percent cover of *Ribes inerme* (Rydb.) and *Castilleja* spp. were square root transformed since a high number of values were less than 20%. Tested variables included those in each category: site, tree (> 1.37 m tall), groundcover, alternate host, and meteorological data (Appendix I, Tables 1.11 – 1.14). For all logistic and linear models, we first screened each category of variables using PROC GLMSELECT with selection=lasso (least absolute shrinkage and selection operator) (stop=sbc choose=sbc [specifies Schwarz criterion as a stopping criterion]) with nsamples=1000 (modifies number of samples used to 1000). Selected variables had to be in at least 20% of those 1000 models. Next, selected variables were incorporated into a model using PROC GLIMMIX (with /s dist=binary to code for the logistic models) with study area as a random effect. Using backward elimination, we manually decided which variable to remove using p<0.001 for significance and watched for large changes in regression coefficients, making sure that there wasn’t a problem with multicollinearity. To further eliminate variables, we used best subsets regression (PROC REG with /best=5 selection=rsquare b [computes estimated regression coefficients for each model selected]) to examine R-squared values for the various model combinations. For logistic models a Wilcoxon rank sum test, with critical level of significance set as $P < 0.0001$, was examined and for linear regression models, Pearson correlations (using PROC CORR), with critical level of significance set as $P < 0.0001$, and scatter plots were examined to review the response distribution to ensure lack of high leverage. For the logistic models, the relationship between fixed effect variables and response variable was plotted using means of all other fixed variables and the 5^{th}, 25^{th}, 50^{th}, 75^{th}, and 95^{th} percentiles of the plotted variable (Figures 1.6, 1.7, and 1.8). Predicted values were back transformed.

3. Results

3.1. Limber pine stand structure and characteristics

Throughout the study, 508 plots (82.3 ha) were established in twenty-five study areas. Surveyed plots ranged in elevation from 826 to 3,140 m and averaged 2,376 m (Table 1.1). Most plots were located on backslopes (40%) and occurred on north aspects (36%) with an average slope of 19% (Appendix I, Table 1.6). Stands were generally open canopy with scattered individuals and/or scattered clumps (64%) (Appendix I, Table 1.6). Grazing was the most common site disturbance and occurred on 56% of plots (Appendix I, Table 1.6). Other site disturbances included tree cutting on 10% of plots, while other human disturbance occurred on 10 %, and fire on 8% of plots (Appendix I, Table 1.6).

Over 38,700 trees >1.37 m in height were examined, of those, 22,700 were limber pines. Limber pine was found in association with Douglas-fir on 206 plots, lodgepole pine on 185 plots, aspen on 170 plots, Rocky Mountain juniper on 133 plots, ponderosa pine on 98 plots, subalpine fir on 86 plots, Engelmann spruce on 64 plots, whitebark pine on 13 plots, and Utah juniper, Rocky Mountain maple, and white spruce on five or less plots. Overall, based on plot means, limber pine made up 69% of total stand density (stems/ha) and 75% of the total average basal area (m^2/ha). Mean DBH of live limber pine ranged from 8.0 (s.d. 1.6) to 16.3 (s.d. 5.5) cm, and averaged 11.9 (s.d. 4.9) cm, while mean overall DBH of all other live species was 9.5 (s.d. 6.1) cm (Table 1.1). Mean basal area (m^2/ha) of live limber pine ranged from 2.6 (s.d. 1.7) m^2/ha to 10 (s.d. 4.9) m^2/ha and averaged 5.8 (s.d. 5.0) m^2/ha, while basal area of all other species averaged 4.5 (s.d. 6.1) m^2/ha (Table 1.1). Mean density of live limber pine ranged from 222 to 502 stems/ha and was 311 (s.d.168) stems/ha, overall, while mean density of all other species was 291 (s.d. 340) stems/ha (Table 1.1).

3.2. Limber pine health status

Only half (50%) of limber pines were classified as healthy (0 to 5% of crown or stem showing symptoms or was damaged), 26% were declining or dying, and 24% were dead (Figure 1.2). For comparison, 69% of all other pines were healthy, with 14% declining or dying, and 17% were dead (Appendix I, Figure 1.11). In ten study areas, mostly in the northern half of all the study areas, less than 50% of limber pines were classified as healthy, with only 16% and 20% of limber pines classified as healthy, compared to 85% and 51% of other pines, in the southern Absaroka Range and Wind River Reservation, respectively (Figure 1.2). Only one plot (Wind River Reservation) exhibited 100% mortality of limber pine. White pine blister rust, alone, accounted for 61% of declining and dying limber pine while dwarf mistletoe, alone, accounted for 19% (Figure 1.3). Bark beetles, alone, accounted for 52% of limber pine mortality, WPBR for 8% and dwarf mistletoe for 4% (Figure 1.3). An additional 17% of limber pine was dead due to any combination of the three damage agents and 16.9% of that included bark beetles (Figure 1.3). Fourteen percent of limber pine was declining or dying due to other damage agents or unknown reasons while 19% were dead from the same (Figure 1.3).

3.2.1. Diseases, insects, and damages

White pine blister rust on live limber pine was widespread and was the most common damage agent, occurring in 23 of the 25 study areas and on 73% of plots. In eight study areas, WPBR was present in 100% of plots (Figure 1.4a). Overall, 26% (± 2.3 half approx. LSD) of live limber pine was infected with 12.2% exhibiting stem cankers. Mean incidence ranged from 0% in the Sierra Madre and Terry Badlands, to 72% in the Southern Absaroka Range (Figure 1.4a). Evidence of bark beetle-caused mortality in limber pine was found in all 25 study areas and on 75% of plots (Figure 1.4b). Overall, 18% (± 1.8 half approx. LSD) of limber pine (Figure 1.4b), and other pines at 17% (± 2.1 half approx. LSD), were successfully attacked by bark beetles, while 1% of limber pines exhibited pitchout (unsuccessful mountain pine beetle attack) and 0.3% exhibited symptoms of a strip attack. Bark beetle-caused mortality was highest in the northern Medicine Bow Mountains at 35%. Limber pine dwarf mistletoe occurred within 20 study areas and was present on 29% of plots (Figure 1.4c). Overall, 9% (± 1.9 half approx. LSD) of live limber pine and 9% (± 2.3 half approx. LSD) of other pines, were infected with dwarf mistletoe. The highest incidence occurred in Boulder County and less than 1% of limber pines were infected with dwarf mistletoe in the Bighorn Mountains while no dwarf mistletoe was found on other pines in the same study areas. Of infected limber pines, 50% were lightly infected (DMR of 1-3) and 50% were heavily infected (DMR of 4-6).

When looking overall, at a comparison based on plot and study area means, of the same 13 study areas previously monitored by Kearns and Jacobi (2007), incidence of WPBR has increased from 20% in 2002-2004 to 26% (p-value <0.0001) in 2011-2012 (Figure 1.5). Both occurrence and incidence of bark beetles increased 64% (p-value <0.0001) and 17% (p-value <0.0001), respectively (Figure 1.5). While dwarf mistletoe occurrence and incidence increased

8% (p-value <0.0280) and 2% (p-value <0.2956), respectively, the increase was not significant (Figure 1.5).

Other diseases and damages on the evaluated limber pines were infrequent but did occur on 41% of the 508 plots and occurred in all study areas. Those that did infect or damage 5% or more of the tree included twig beetles which occurred in 22 study areas, on 105 plots, and on 1.6% of trees; wild animal damage (e.g., porcupine or squirrel chewing and deer or elk rubbing) and abiotic damage occurred in all 25 study areas and on 104 and 93 plots, respectively, and 1.6% of limber pine, each (Appendix I, Figure 1.12).

3.3. Model results

3.3.1. Variables that predict occurrence and incidence of WPBR

We used logistic regression to determine the variables that predict the occurrence of WBPR on a subplot. Variables in the site (plot), tree, ground cover, alternate host, and meteorological categories, were selected in at least 20 percent of the 1000 models after screening each category. Variables selected in the final model include $\log_{10}$ stems/ha of limber pine and mean May precipitation (mm) (Table 1.2). Both $\log_{10}$ stems/ha of limber pine and mean May precipitation (mm) had a positive influence on occurrence of WPBR (Figures 1.6a and b). When eliminating meteorological variables, those selected in the final model included northing (latitude), elevation (m), and $\log_{10}$ stems/ha of limber pine (Table 1.2).

Linear regression determined the variables that predict the incidence, or percent of live and dead limber pine stems with WPBR on a subplot. Category screening produced 126 variables in all categories (plot, tree, ground cover, alternate host, and meteorological) that were selected in at least 20 percent of the 1000 models. Of those variables, 17, largely meteorological, were correlated with percent of limber pine stems with WPBR, with a Pearson correlation coefficient (P) of at least ± 0.20 (Table 1.5). However, mean May precipitation (mm) ($P = 0.39$, p-value <0.0001) was the only variable selected in the final model (Table 1.2).

3.3.2. Variables that predict occurrence and incidence of dwarf mistletoe

Using logistic regression, we were able to determine the variables that predict occurrence of dwarf mistletoe on live and dead limber pine in a subplot. The only variable selected in the final model included the positive influence of $\log_{10}$ stems/ha of limber pine (Table 1.3, Figure 1.7).

Linear regression determined the variables that predicted the incidence, or percent of limber pine stems with dwarf mistletoe on a subplot. Category screening produced 64 variables, mostly meteorological, that were selected in at least 20 percent of the 1000 models. Of those, only seven variables were correlated with percent limber pine stems with dwarf mistletoe, with P's of at least ± 0.15 (Table 1.5). Variables selected in the final model include $\log_{10}$ stems/ha of limber pine ($P = 0.17$, p-value <0.0001) and $\log_{10}$ stems/ha of other pines ($P = -0.11$, p-value <0.0003) (Table 1.3).

3.3.3. Variables that predict occurrence and incidence of bark beetles

The occurrence of bark beetles on limber pine a subplot was modeled with logistic regression analysis and $\log_{10}$ basal area (m^2/ha) of limber pine was the only variable selected in the final model (Table 1.4.) Basal area of limber pine had a positive influence on occurrence of bark beetles (Figure 1.8).

Linear regression determined the variables that predicted the incidence, or percent of limber pine stems with bark beetles on a subplot. Category screening produced 94 variables that were selected in at least 20 percent of the 1000 models. Of those, fourteen variables were correlated with percent limber pine stems with bark beetles, with P's of at least ± 0.20 (Table

1.5). Variables selected in the final model include proportion of limber pine with DBH >20 cm (P = 0.44, p-value <0.0001) and $\log_{10}$ basal area (m^2/ha) of other pines (P = -0.08, p-value <0.0014) (Table 1.4). No site or meteorological variables were selected in either the logistic or linear regression models predicting bark beetles on limber pine.

4. Discussion

4.1. Limber pine stand conditions, health, and damage agents

White pine blister rust, bark beetles, and dwarf mistletoe are the major damage agents on limber pine in the southern and central Rocky Mountains. Each agent varies in the length of time between infection and mortality. While bark beetles during epidemic levels can rapidly overcome a tree's defense system within one year, it takes longer for WPBR (years to decades) (Geils et al. 2010) and dwarf mistletoe (10 – 40 years for larger trees) (Hawksworth and Geils 1990) and depends on severity of infection. Limber pine decline in health and mortality in the southern and central Rocky Mountains increased from 2002 to 2012, primarily due to WPBR and bark beetles. Density of live limber pine (311 stems/ha) is low compared to 546 stems/ha, density of evaluated limber pine by Kearns and Jacobi (2007) in 2002-2004. Mean basal area (m^2/ha) of live limber pine is also considerably lower at 5.8 m^2/ha compared to 22 m^2/ha from a study of limber pine in the Rocky Mountains of Alberta, Canada (Smith et al. 2013). Since Kearns and Jacobi (2007) surveyed limber pine stands in 2002-2004, limber pines classified as declining, dying, or dead in the same study areas has increased 28% (Appendix I, Table 1.8). A majority of recent mortality in limber pine is attributed to bark beetles, since bark beetles alone or in combination with other major damage agents were noted in 69% of dead limber pine and incidence has increased 17% in the same evaluated study areas by Kearns and Jacobi (2007). The increase in evidence of bark beetle attacks can largely be explained by the most recent mountain pine beetle epidemic. Since mountain pine beetles prefer larger diameter trees (Safranyik and Carroll 2006), this may partially explain the 16 m^2/ha difference in basal area of limber pine in Alberta (Smith et al. 2013), where bark beetles accounted for only 4% of limber pine mortality. However, mortality of other pines on our plots, also suitable hosts for mountain pine beetle, was 8% less than limber pine with all mortality attributed to bark beetles, indicating that the addition of WPBR is causing an increase in mortality in limber pines as compare to other pines.

White pine blister rust accounted for the majority, 67%, of declining and dying limber pine and incidence has increased 6% in the 13 study areas previously monitored by Kearns and Jacobi (2007), indicating that WPBR is intensifying in existing areas. Occurrence and incidence of WPBR is higher in the more northern study areas, which is consistent with WPBR being in these areas for longer. The southern Absaroka Range, one of the more northern study areas with only 16% of limber pines considered healthy, had the highest incidence of WPBR at 72% and had a high incidence of bark beetle mortality at 25%. Interestingly, just as Kearns and Jacobi (2007) did not find WPBR in the Sierra Madre Range and found very low incidence, about 1%, in the remainder of the Medicine Bow Mountains, we also found no WPBR in the Sierra Madre and only about 3% in the remaining areas of the Medicine Bow Mountains. The topography of Wyoming varies significantly, allowing for unique meteorological events within and among nearby mountain ranges, and since meteorological conditions regulate spore production and dissemination, it possible that the Medicine Bow Mountains lack conducive conditions for WPBR infection. It may also be possible that the limber pines in this area, possess some WPBR resistance traits, but this calls for further examination.

Limber pine dwarf mistletoe, the third most damaging agent to limber pine with a mean incidence of 9%, did not show significant increase in the study areas previously monitored by

Kearns and Jacobi (2007). However, incidence did vary between study areas from very little dwarf mistletoe in the Bighorn Mountains, <1%, to 27% in Boulder County, Colorado. Taylor and Mathiason (1999) indicate that limber pine dwarf mistletoe is limited in dense stands due to lack of light available for seed production and decreased host vigor due to competition, however, Boulder County, with the highest mean incidence of dwarf mistletoe, also had one of the highest overall densities of limber pine at 435 stems/ha and all other species at 827 stems/ha. In general, dwarf mistletoe was only present when other species of dwarf mistletoe were present on lodgepole and or ponderosa pine.

4.2. Statistical models

4.2.1. White pine blister rust

The results of our logistic regression model predicting WPBR occurrence indicated that stems/ha of limber pine and mean May precipitation (mm) were important variables in predicting WPBR occurrence, while our linear regression model predicting incidence of WPBR only indicated mean May precipitation as an important predictor variable. The positive influence of stems/ha of limber pine is natural, since limber pine is a primary host of WPBR. The positive influence of mean May precipitation may be explained by increased spring and early summer opportunities for infection of *Ribes* or other alternative hosts or possibly better aecia production during conditions of increased moisture. Precipitation as a predictor variable is supported by modeling efforts by Smith and Hoffman (2001) who indicated that mean summer precipitation was an important in predicting both occurrence and incidence of WPBR in whitebark pine. Since WPBR infection requires conditions cool, humid conditions for infection, as other studies found (Larson 2010, Dunlap 2012, Kearns et al. 2013), we expected addition meteorological variables, such as relative humidity and temperature, to predict occurrence and incidence of WPBR.

When eliminating meteorological variables, we found northing (latitude) and elevation to be important predictor variables of occurrence of WPBR. Northing was also positively correlated with WPBR occurrence, supporting the temporal relationship with length of time WPBR has been present in the study areas. Several studies have indicated that elevation is either correlated with or an important factor in predicting WPBR (Smith and Hoffman 2001, Duriscoe and Duriscoe 2002, Hunt 2005, Kearns and Jacobi 2007, Dunlap 2012). While studies by Hunt (2005) indicate that white pines at higher elevations are less prone to WPBR than at low elevations, we actually found a slight positive correlation and relationship with elevation when meteorological variables were left out. This could be related to the general increase in moisture with elevation in the Rocky Mountains and higher frequency high elevation forests within cloud moisture during spring or late summer infection periods. While we found no additional relationships with any other site or stand variables, other studies have done so. Site characteristics, such as topography (Duriscoe and Duriscoe 2002), slope (Kearns and Jacobi 2007, Kearns et al. 2013), slope position (Larson 2010, Kearns et al. 2013), presence of *Ribes* (Campbell and Antos 2000, Duriscoe and Duriscoe 2002, Kearns et al. 2013), and stream density (Kearns et al. 2013) and stand characteristics, such as canopy cover (Campbell and Antos 2000), tree diameter (Smith and Hoffman 2001, Kearns and Jacobi 2007), stand density (Larson 2010), and percentage of large trees (Kearns et al. 2013) have been found to either be correlated with or impact WPBR.

4.2.2. Dwarf mistletoe

Occurrence of dwarf mistletoe is largely impacted by temperature restrictions on flowering and thus reproduction and long distance dispersal by birds, a factor we did not measure. In addition it is plausible that dwarf mistletoe occurrence may be a result of past fire history or glacial refugia. Thus, our dwarf mistletoe models did not show strong relationships with any of our measured variables, likely for these reasons. Our logistic regression model, predicting occurrence of limber pine dwarf mistletoe, indicated that stems/ha of limber pine was a predictor variable. Since limber pine is an ideal host of dwarf mistletoe, we would naturally expect the predicted positive relationship of increased density with dwarf mistletoe occurrence. However, Taylor and Mathiason (1999) indicated that tree to tree spread of limber pine dwarf mistletoe is positively correlated with less dense, multistoried stands of suitable hosts (Taylor and Mathiason 1999). While we found no relationships with meteorological variables and little is known about the impact of climate on the distribution of limber pine dwarf mistletoe, the most limiting factor may be minimum temperature (Hawksworth and Wiens 1996). Barrett et al. (2012) found that the distribution of hemlock dwarf mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones) was related to growing degree days, indirect and direct solar radiation, rainfall, snowfall, slope, and minimum temperatures. We also found no relationships with site characteristics, but Hawksworth and Wiens (1996) suggested that elevation, topographic position, slope steepness, and aspect may influence the distribution of dwarf mistletoe.

Our linear regression model predicting percent limber pine stems infected with dwarf mistletoe indicated that stems/ha of limber pine and stems/ha of other pines were predictor variables. The R^2 of the fixed effect variables was only 0.04 so we do not feel this model has much applicability especially since no site or meteorological variables were utilized.

4.2.3. Bark beetles

The results of our logistic regression model predicting bark beetle occurrence on limber pine indicated basal area (m^2/ha) of limber pine was the only predictor variable and had a positive influence. The results of our linear regression model predicting incidence of bark beetles on limber pine indicted that proportion of limber pine with DBH >20 cm and basal area (m^2/ha) of other pines were important predictor variables. Since all pines are suitable host for bark beetles and mountain pine beetle prefers larger diameter trees (Safranyik and Carroll 2006), we would expect positive relationships with both basal area of limber pine and proportion of limber pine with DBH>20, and a positive relationship with basal area of other pines. Similarly, Negron et al. (2008) found a correlation between basal area of ponderosa pine with dbh > 25.4 cm and mountain pine beetle attacks, while Larson (2010) found a correlation between mountain pine beetle attacks on whitebark pine and low-density, larger diameter stands. While others have indicated that meteorological variables, including temperature and precipitation, may be important in predicting bark beetles (Carroll et al. 2003, Larson 2010), no meteorological variables predicted either occurrence or incidence of bark beetles on limber pine. While we did not find dwarf mistletoe to predict occurrence or incidence of bark beetles, Geils et al. (2002) alludes to the potential for dwarf mistletoe to be a predisposing factor to attack by mountain pine beetle and proposes that moderately infected trees may be more likely to be attacked by the mountain pine beetle than uninfected trees.

4.3. Implications for management

The increase in spread and intensification of WPBR in limber pine, combined with the recent mountain pine beetle epidemic have impacted limber pine stands by causing increased decline in health, and mortality throughout the southern and central Rocky Mountains. Potential loss of limber pine from some populations could have cascading ecosystem effects in these areas. In the northwestern U.S., where WPBR has been present longer, the native range of western white pine (*Pinus monticola* Douglas ex D. Don) has declined and allowed for replacement by late successional species (Schwandt et al. 2013). Our results indicate areas that may be considered a priority for monitoring, management, and restoration. Areas where incidence of either WPBR or bark beetles is high, and particularly areas with high incidences of both, are areas of concern. While it may possible for limber pine stands with WPBR to recover to some level if genetic resistance exists, those trees may be at risk of bark beetle-induced mortality. Additionally, as WPBR kills both seedlings and mature trees and bark beetle induced mortality occurs in mature, cone-bearing limber pine, few cone and seed producing trees may be left to sustain the stand. Clark's nutcracker may not return to these decimated stands. For whitebark pine, an estimated basal area of 5 m^2/ha is required to produce the amount of cones needed for Clark's nutcracker to return to a stand (McKinney et al. 2009), and while we are not sure how it applies to limber pine, 32% of our study areas fall below this mean.

While our results provide meteorological variables that influence both WPBR and dwarf mistletoe, the added unknown of how future climate regimes may impact these damage agents and their host should be considered. Recent increase in mortality in western U.S. trees may be the result of regional warming (van Mantgem 2009). Since white pine blister rust infection is induced by cool temperatures and high relative humidity, if warmer and drier metrological conditions prevail, opportunities for WPBR infection may diminish (Sturrock et al. 2011). Increased temperature could allow for an increase in suitable habitat, expanding in both latitude and elevation, for bark beetles (Bentz et al. 2010). Predicting the impact of climate change on dwarf mistletoe is more difficult and depends on host movement and bird dispersal. If host dispersal is affected, it is possible that dwarf mistletoe may not be able to adapt (Way 2011).

Maintaining limber pine stands is a priority for preserving potentially genetically WPBR-resistant trees. While our statistical models indicates a positive influence of density of limber pine on both WPBR and dwarf mistletoe, and a positive influence of basal area of limber pine, we might suggest thinning stands to increase vigor, but taking care to leave healthy, seed producing trees. In stands with little impact by WPBR, stand management for multiple age classes may encourage regeneration (Schoettle and Sniezko 2007) and help to sustain stands during bark beetle attacks. Collection of seed and testing for WPBR resistance to outplant WPBR resistant stock has become an increasingly viable restoration option, particularly since complete resistance has recently been identified in limber pine (Schoettle and Sniezko 2007, Schoettle et al. 2014).

Areas where occurrence and incidence of WPBR and bark beetles is low may not need intervention but should be monitored. In Colorado, our results indicate that occurrence and incidence of WPBR remains low, and while WPBR has been spreading south through Colorado, modeling efforts by Kearns et al. (2014) indicate that future occurrence and incidence in the southern Rocky Mountains may be limited due to environmental conditions. Additionally, in Colorado, areas of mountain pine beetle-caused mortality increased by only 3,200 ha in 2013, versus 12,500 ha in 2012, and 57,000 ha in 2011, indicating that the epidemic is in decline (2013 Forest Health Aerial Survey). What drives the periodicity of mountain pine beetle outbreaks is not well understood, but within the last century, outbreaks appeared in Colorado limber pine areas on one or more pine host about 2-3 times. Thus, managing and monitoring limber pine stands for resiliency against future insect and disease outbreaks, keeping in mind changing climate regimes, should be a priority.

Tables and Figures

Table 1.1: Summary of plots, mean elevation, diameter breast height (DBH) (cm), basal area (m^2/ha) and stems/ha of live limber pine and all other live species in limber pine stands on 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

State, geographic range, and study area (Ownership)	Plots[1]	Mean elevation (m)	Live limber pine n	DBH[2] (cm) mean	DBH[2] (cm) std	Basal area[3] (m^2/ha) mean	Basal area[3] (m^2/ha) std	Stems/ha mean	Stems/ha std	Live all other species n	DBH (cm) mean	DBH (cm) std	Basal area (m^2/ha) mean	Basal area (m^2/ha) std	Stems/ha mean	Stems/ha std
Colorado																
Front Range																
Boulder County (Boulder County)	14	2735	14	11.8	3.3	6.9	4.3	435	188	14	12.7	3.1	12.6	6.1	827	572
North (NF)*	25	2669	24	12.5	5.4	8.1	11.1	328	228	24	12.6	5.0	11.4	7.8	551	350
Wyoming																
Laramie Mtns																
Pole Mtn (NF)*	24	2544	24	9.0	3.1	3.3	2.6	302	177	22	11.0	4.7	11.0	7.1	625	292
East (NF)*	24	2347	24	9.4	2.4	3.7	2.2	312	163	24	11.8	6.2	9.1	9.2	388	386
West (NF)*	24	2482	24	12.3	3.8	4.5	3.1	245	137	22	11.2	4.9	9.2	7.3	509	378
Muddy Mtn (BLM)*	21	2339	21	12.0	4.2	6.6	4.3	293	132	19	8.0	4.5	2.6	2.8	285	355
Medicine Bow Mtns																
South (NF)*	24	2633	24	10.2	3.7	3.4	2.5	246	94	21	10.3	6.9	2.8	3.1	230	212
North (NF)*	24	2797	24	12.8	4.6	6.1	4.8	264	121	20	10.1	4.1	3.7	3.0	230	170
Sierra Madre (NF)*	24	2736	24	11.1	4.2	5.0	5.3	263	160	18	10.3	7.7	2.6	4.1	191	303
Sweetwater Basin																
Shirley Mtns (BLM)*	24	2424	24	10.0	2.5	5.7	2.2	425	196	11	7.8	4.4	0.5	0.6	51	40
Ferris Mtns (BLM)*	6	2293	6	16.3	5.5	9.0	3.8	256	32	5	9.8	9.5	1.4	2.0	33	32
Green Mtns (BLM)*	24	2516	24	10.5	3.8	7.4	4.5	472	188	15	14.0	7.4	3.0	3.5	169	250
Beaver Divide[5] (BLM)	16	2287	16	11.5	4.2	6.8	5.5	367	123	6	8.1	8.3	0.6	0.7	73	92
Wind River Range																
South (NF)	27	2599	27	12.7	4.4	6.5	4.9	297	168	21	10.5	8.8	2.4	2.6	194	239
Reservation (Tribal)*	18	2654	17	10.0	3.4	4.7	6.9	222	140	16	11.0	8.2	3.8	7.1	186	308
North (NF)	28	2503	28	10.1	4.7	4.1	3.8	255	129	25	8.9	5.1	3.8	5.1	306	474
Absaroka Range																
South (NF)*	20	2462	20	15.0	3.4	5.8	3.3	230	107	17	6.2	4.0	2.6	4.9	259	213
Shoshone Canyon[6] (BLM)	17	2083	17	8.7	4.3	2.6	1.7	301	146	14	4.1	3.9	0.8	1.7	104	84
North (NF)	24	2054	24	14.9	7.4	5.5	3.8	269	150	18	9.6	6.4	1.5	2.1	126	157
Bighorn Basin (BLM)	11	1918	11	11.0	3.2	5.0	2.9	322	110	11	4.8	2.1	1.2	2.2	230	245
Bighorn Mtns																
East (BLM)	17	2404	17	11.8	4.5	5.9	4.0	328	193	16	10.4	8.0	4.1	7.9	209	314
South (NF)	20	2518	20	14.6	5.0	7.9	4.3	290	153	19	10.4	6.4	3.0	3.6	144	93
North (NF)	24	2478	24	16.0	7.0	9.1	6.5	349	213	24	6.7	4.4	1.7	2.0	223	291
Montana																
Pryor Mtns (NF, BLM)	20	2076	20	16.3	6.4	10.0	4.9	331	116	20	6.3	3.7	2.3	3.1	290	260
Terry Badlands (BLM)	8	858	8	8.0	1.6	3.9	1.6	502	137	7	4.3	1.9	0.6	0.8	164	126
Total	508	2376	506	11.9	4.9	5.8	5.0	311	168	429	9.5	6.1	4.5	6.1	291	340

[1]One plot = three 60 x 6 m subplots placed at random bearings with a 30 x 6 m WPBR alternate host plot at the end of each subplot.
[2]Diameter breast height was measured 1.37 m above the ground on the uphill side of the tree.
[3]Cross sectional area of a tree at DBH (1.37 m above the ground).
*Indicates previously monitored stands.
[4]Includes Beaver Rim, Crooks Mountain, and the Rattlesnake Range.
[5]Includes Cedar Mountain, Rattlesnake Mountain, and Sheep Mountain.

Table 1.2: Logistic regression predicting occurrence (y/n) of WPBR on limber pine on a subplot and linear regression for predicting percent limber pine stems with WPBR on a subplot. Models fit using PROC GLIMMIX (with /s dist=binary for the logistic model) with study area as a random effect. R^2 value obtained using PROC REG with /best=5 selection = rsquare b, and applies only to the fixed effects. The critical level of significance is set at $p<0.001$.

Model	Parameter	Estimate	Standard error	AUC	Classification accuracy	R^2
Occurrence of WPBR on a subplot	Intercept	-9.8932	1.1612	0.70	0.73	
	Log_{10} stems/ha of limber pine	1.5812	0.2349			
	Mean May precipitation (mm)	0.2789	0.0390			
Occurrence of WPBR on a subplot (no meteorological variables)	Intercept	-41.6886	10.6808	0.65	0.64	
	Northing (m)	0.0730	0.0220			
	Elevation (m)	0.0017	0.0004			
	Log_{10} stems/ha of limber pine	1.5803	0.2344			
Percent stems infected with WPBR (sqrt)	Intercept	-5.9398	1.0298			0.15
	Mean May precipitation (mm)	0.3972	0.0388			

Table 1.3: Logistic regression predicting occurrence (y/n) of dwarf mistletoe on limber pine on a subplot and linear regression for predicting percent limber pine stems with dwarf mistletoe on a subplot. Models fit using PROC GLIMMIX (with /s dist=binary for the logistic model) with study area as a random effect. R^2 value obtained using PROC REG with /best=5 selection = rsquare b, and applies only to the fixed effects. The critical level of significance is set at $p<0.001$.

Model	Parameter	Estimate	Standard error	AUC	Classification accuracy	R^2
Occurrence of dwarf mistletoe on a subplot	Intercept	-6.1202	0.7889	0.60	0.55	
	Log_{10} stems/ha of limber pine	1.6588	0.2736			
Percent stems with dwarf mistletoe (sqrt)	Intercept	-1.3774	0.7499			0.04
	Log_{10} stems/ha of limber pine	1.3431	0.2768			
	Log_{10} stems/ha of other pines	-0.4202	0.0947			

Table 1.4: Logistic regression predicting occurrence (y/n) of bark beetles on limber pine on a subplot and linear regression for predicting percent limber pine stems with bark beetles on a subplot. Models fit using PROC GLIMMIX (with /s dist=binary for the logistic model) with study area as a random effect. R^2 value obtained using PROC REG with /best=5 selection = rsquare b, and applies only to the fixed effects. The critical level of significance is set at $p<0.001$.

Model	Parameter	Estimate	Standard error	AUC	Classification accuracy	R^2
Occurrence of bark beetles on a subplot	Intercept	-1.9717	0.1817	0.55	0.58	
	Log_{10} basal area (m^2/ha) of limber pine	6.9580	0.4353			
Percent stems with bark beetles (sqrt)	Intercept	0.1423	0.2266			0.24
	Proportion of limber pine with dbh >20 cm	0.0376	0.0035			
	Log_{10} basal area (m^2/ha) of all pines	4.6262	0.4257			

Table 1.5: Variables selected in at least 20% of 1000 models during category screening using PROC GLMSELECT, with Pearson correlation coefficients (P) of at least ± 0.2, except square root (percent stems infected with dwarf mistletoe) where correlations are at least ± 0.15.

Model and variables	P	p-value
Square root (Percent stems with WPBR)		
northing	0.22	<.0001
$\log_{10}$ stems/ha of other pine	-0.20	<.0001
12 month moderate or greater drought frequency	-0.28	<.0001
mean May precipitation*	0.39	<.0001
mean June precipitation*	0.21	<.0001
average minimum temperature in January *	-0.28	<.0001
average maximum temperature in January*	-0.23	<.0001
average temperature in November *	-0.21	<.0001
average relative humidity in April*	0.38	<.0001
average relative humidity in May*	0.33	<.0001
average relative humidty in June*	0.32	<.0001
average relative humidity in November*	0.24	<.0001
diffuse short-wave radiation	0.28	<.0001
average relative humidity July-September**	0.20	<.0001
average maximum temperature May-June**	-0.21	<.0001
total precipitation in 2000	-0.20	<.0001
total precipitation in 2006	-0.24	<.0001
Square root (Percent stems with bark beetles)		
proportion of limber pine with dbh ≤ 5 cm	-0.37	<.0001
proportion of limber pine dbh > 20 cm	0.44	<.0001
proportion of limber pine with codominant crown class	0.21	<.0001
$\log_{10}$ basal area (m²/ha) of limber pine	0.50	<.0001
spring frost day*	0.25	<.0001
average temperature in June*	-0.25	<.0001
maximum temperature in the warmest month*	-0.23	<.0001
average temperature in the warmest month*	-0.25	<.0001
average maximum temperature May-June**	-0.21	<.0001
average maximum temperature July-September**	-0.21	<.0001
average minimum temperature July-September**	-0.21	<.0001
average minimum temperature in 2005	-0.21	<.0001
average minimum temperature in 2006	-0.23	<.0001
average minimum temperature in 2010	-0.21	<.0001
Square root (Percent stems with dwarf mistletoe)		
presence of bark peetles on limber pine	0.15	<.0001
presence of WPBR on limber pine	-0.17	<.0001
log10 stems/ha of limber pine	0.17	<.0001
log10 basal area (m²/ha) of limber pine with WPBR	-0.18	<.0001
mean May precipitation*	-0.16	<.0001
2nd principle component monthly precipitation	0.18	<.0001
average precipitation May-June*	-0.15	<.0001

* Based on 30-year averages

** Based on 2000-2012 averages

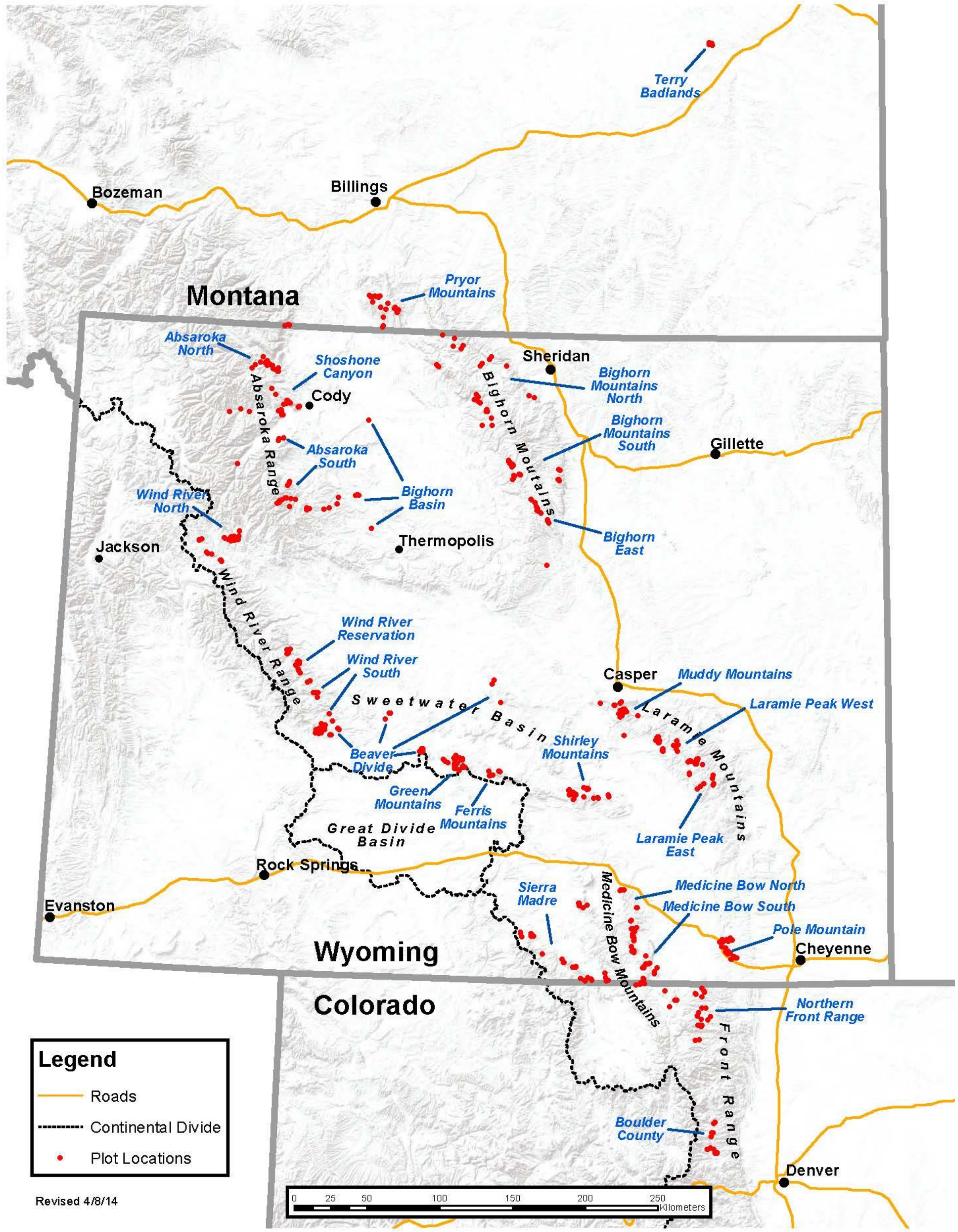


Figure 1.1: Location of limber pine monitoring plots in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

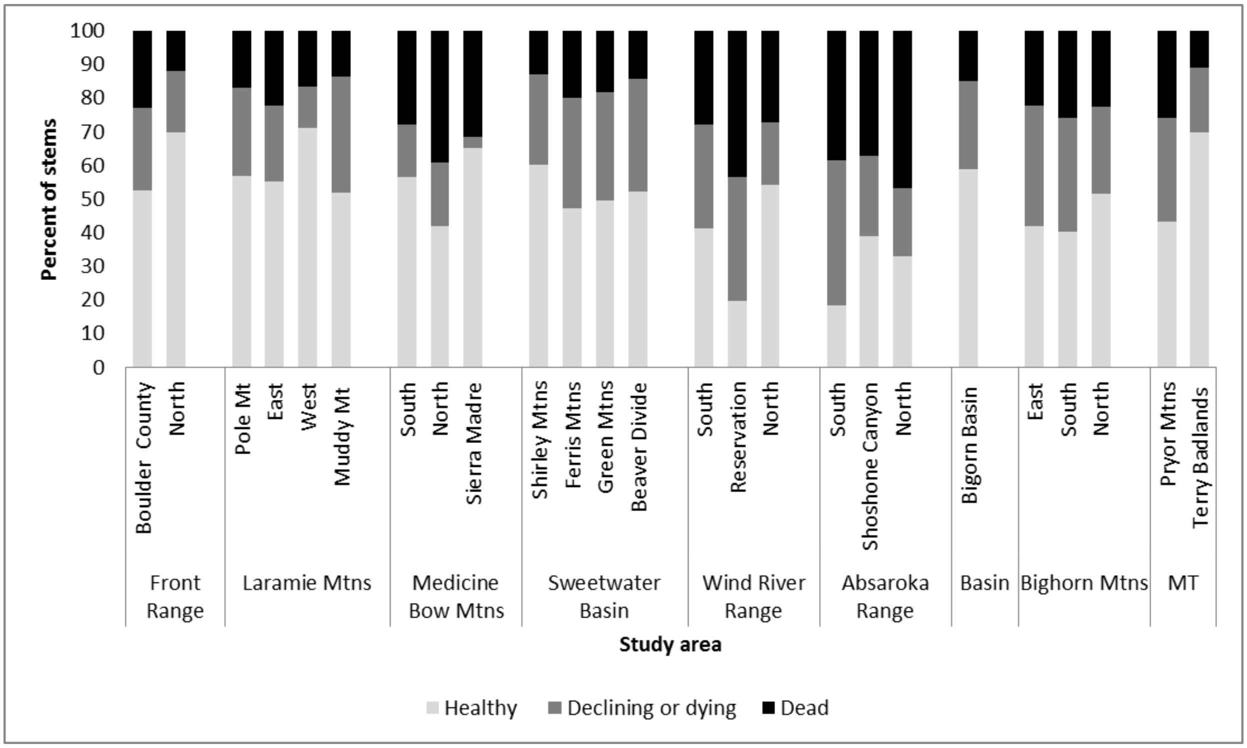


Figure 1.2: Health status of limber pine in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Healthy stems include stems with a health status of 1 and have no visual damage to crown or stem up to 5% damage. Declining stems include stems with a health status of 2 and are categorized as such if 6-50% of crown showing symptoms that indicates it is dead or will be; and dying stems include stems with a health status of 3 and are categorized as such if >50% of crown showing symptoms or is damaged. Dead stems include stems with a health status of 4, recent dead, no green needles, red needles but fines still present, health status of 5, old dead, no fine twigs, no needles, >50% bark still present, or health status of 6, very old dead, no fine twigs, no needles, <50% of bark present.

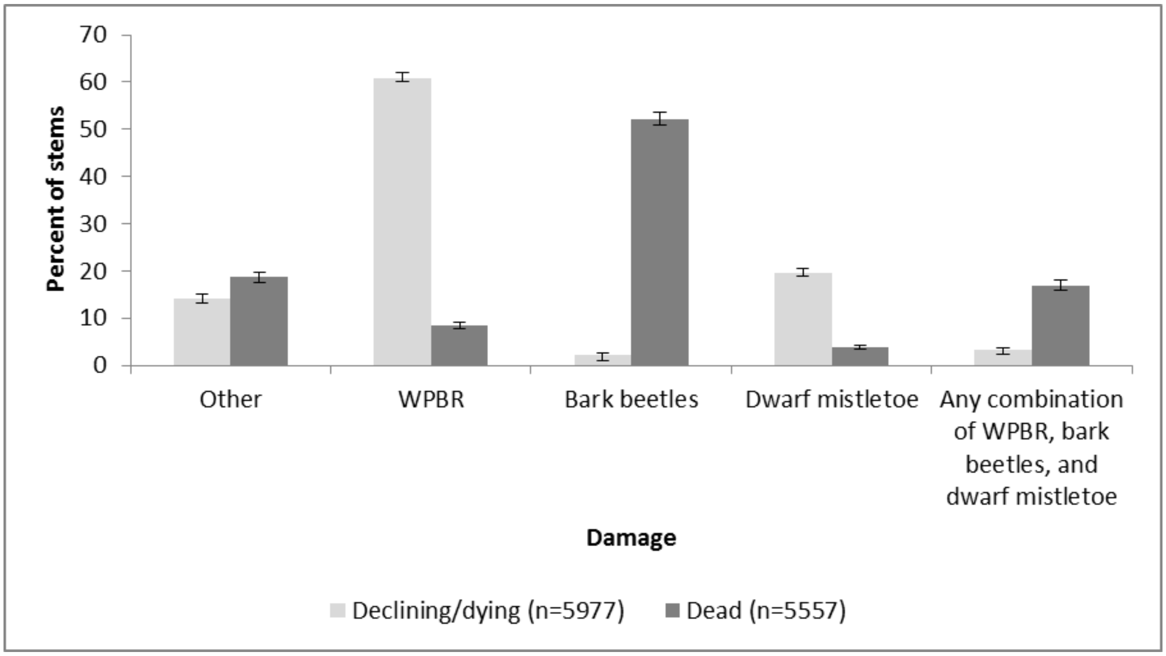
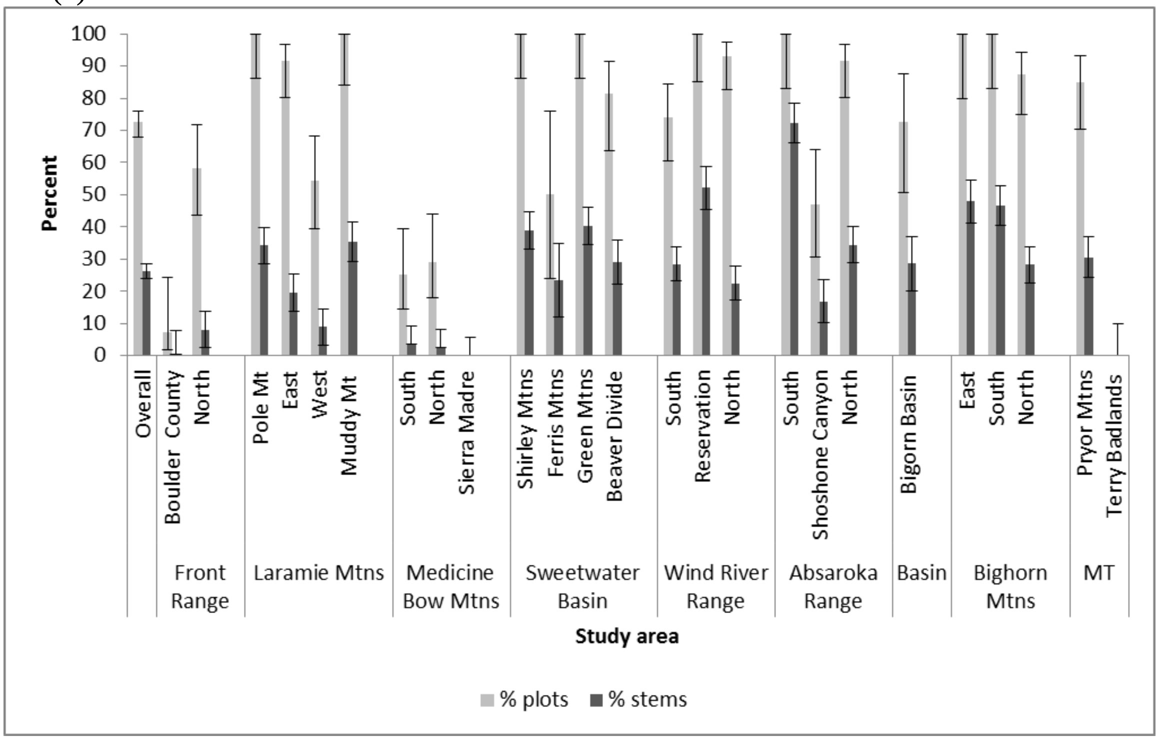
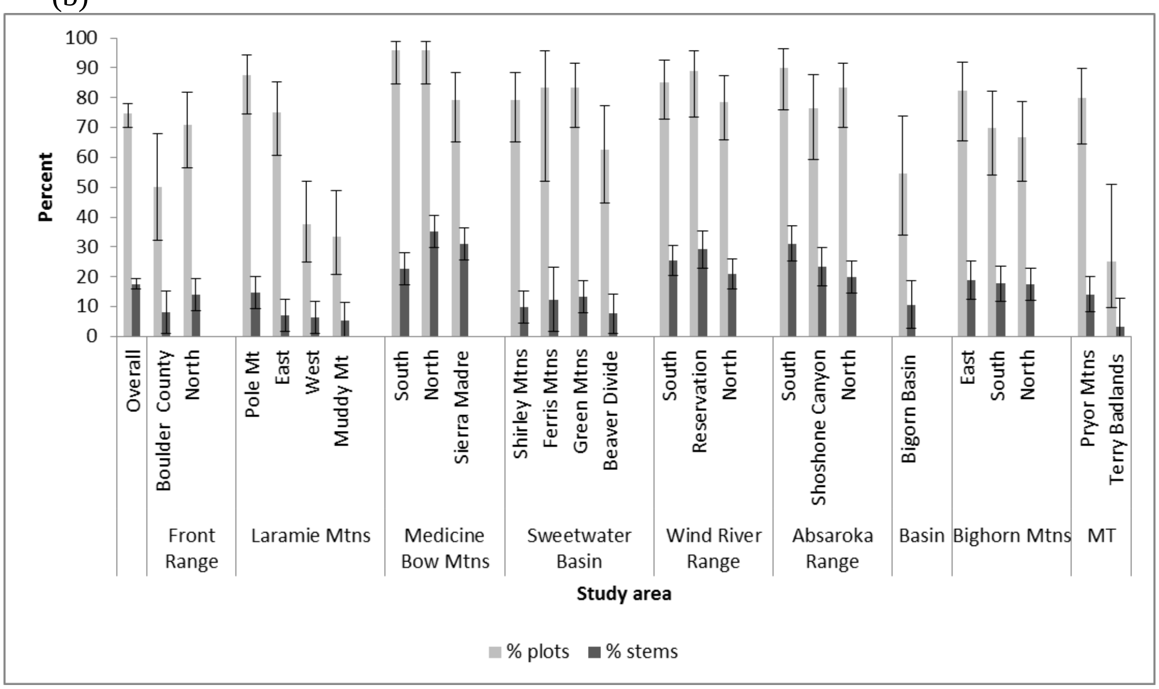


Figure 1.3: Allocation of damage to declining or dying and dead limber pine in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Declining stems include stems with a health status of 2 and are categorized as such if 6-50% of crown showing symptoms that indicates it is dead or will be; and dying stems include stems with a health status of 3 and are categorized as such if >50% of crown showing symptoms or is damaged. Dead stems include stems with a health status of 4, recent dead, no green needles, red needles but fines still present, health status of 5, old dead, no fine twigs, no needles, >50% bark still present, or health status of 6, very old dead, no fine twigs, no needles, <50% of bark present. Error bars are ± 2 standard errors of the percent.

(a)


Percent
Overall
Boulder County
North
Front Range
Pole Mt
East
West
Muddy Mt
Laramie Mtns
South
North
Sierra Madre
Medicine Bow Mtns
Shirley Mtns
Ferris Mtns
Green Mtns
Beaver Divide
Sweetwater Basin
South
Reservation
North
Wind River Range
South
Shoshone Canyon
North
Absaroka Range
Bigorn Basin
Basin
East
South
North
Bighorn Mtns
Pryor Mtns
Terry Badlands
MT
Study area
% plots
% stems

(b)


Percent
Overall
Boulder County
North
Front Range
Pole Mt
East
West
Muddy Mt
Laramie Mtns
South
North
Sierra Madre
Medicine Bow Mtns
Shirley Mtns
Ferris Mtns
Green Mtns
Beaver Divide
Sweetwater Basin
South
Reservation
North
Wind River Range
South
Shoshone Canyon
North
Absaroka Range
Bigorn Basin
Basin
East
South
North
Bighorn Mtns
Pryor Mtns
Terry Badlands
MT
Study area
% plots
% stems

(c)

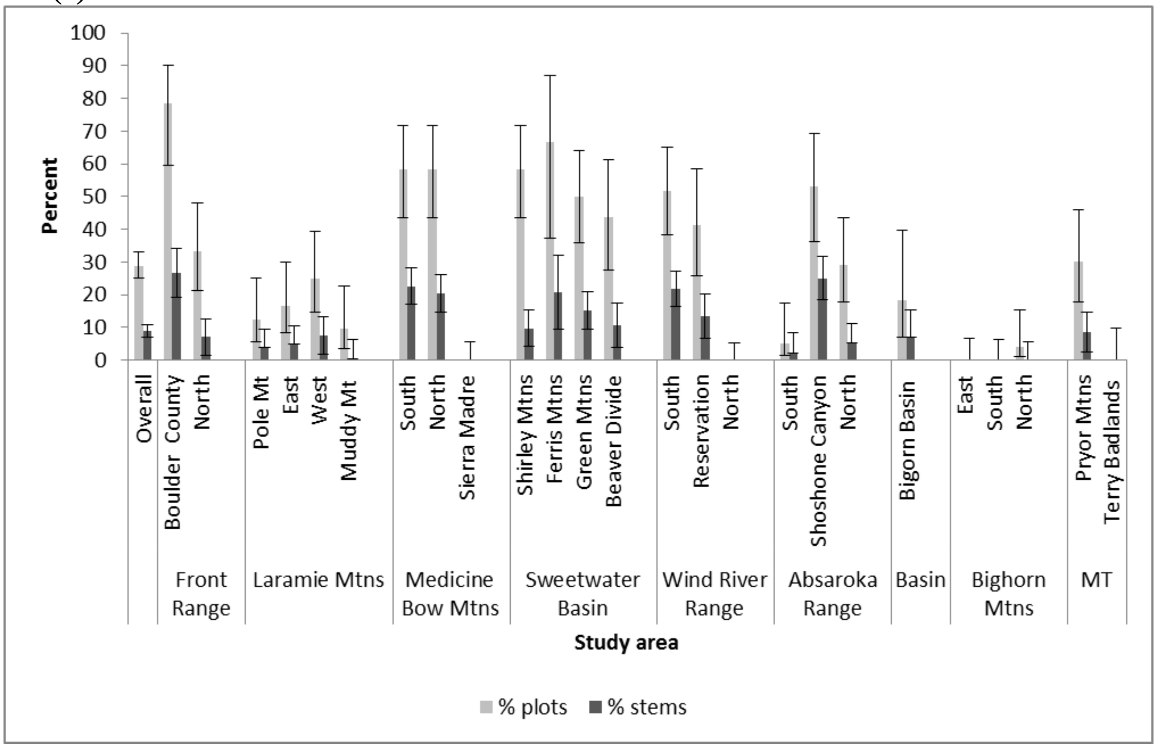


Figure 1.4: Occurrence (percent of plots) (least square means using PROC GLIMMIX) and incidence (percent of stems) (least square means using PROC MIXED) of a) white pine blister rust on live limber pine, b) bark beetles on live and dead limber pine, and c) dwarf mistletoe on live limber pine in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Values are adjusted for study area. Error bars are ± half approximate LSD.

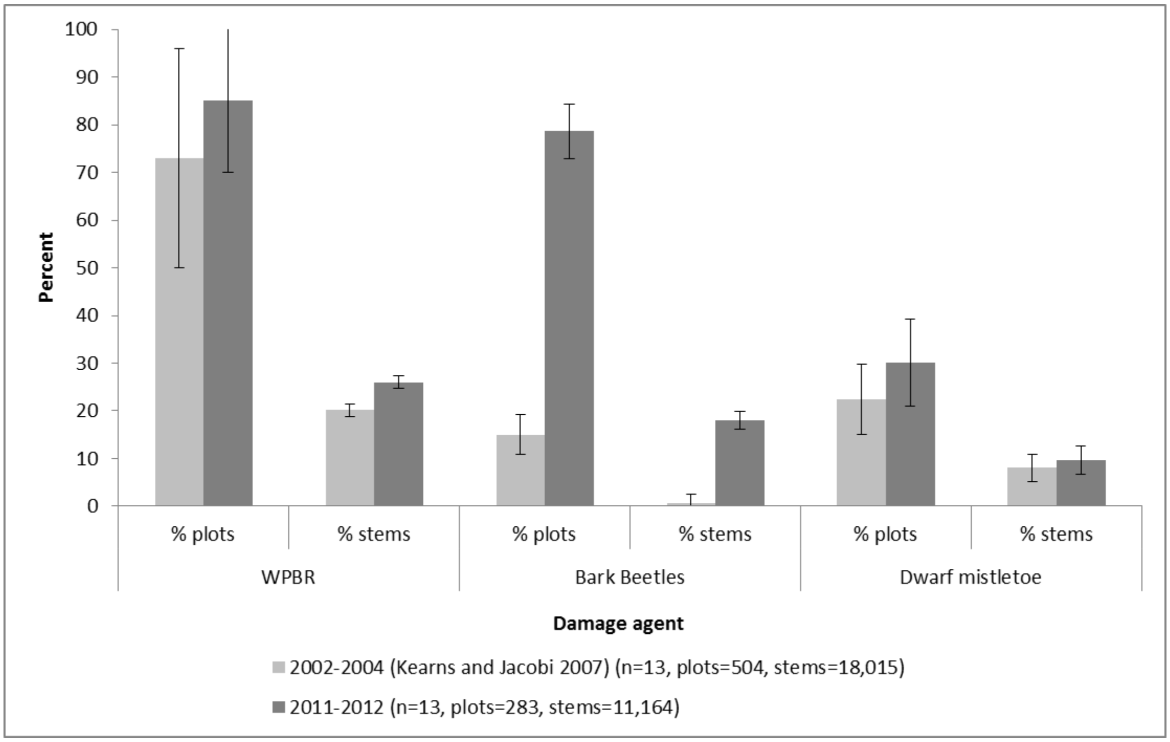
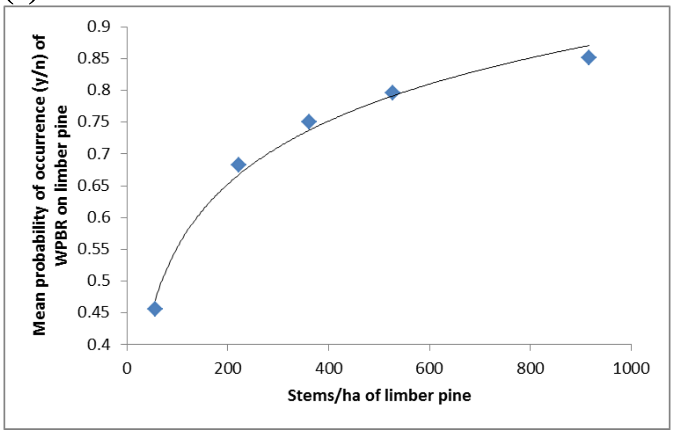


Figure 1.5: A comparison of occurrence (percent of plots) (least square means using PROC GLIMMIX with study area as a random effect) and incidence (percent of stems) (least square means using PROC MIXED with study area as a random effect) of WPBR on live limber pine, bark beetles on live and dead limber pine, and dwarf mistletoe on live limber pine at the study area level (n=13) from a 2002-2004 survey (Kearns and Jacobi 2007) and a survey of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Values are adjusted for study area. Error bars are ± half approximate LSD.

(a)



(b)

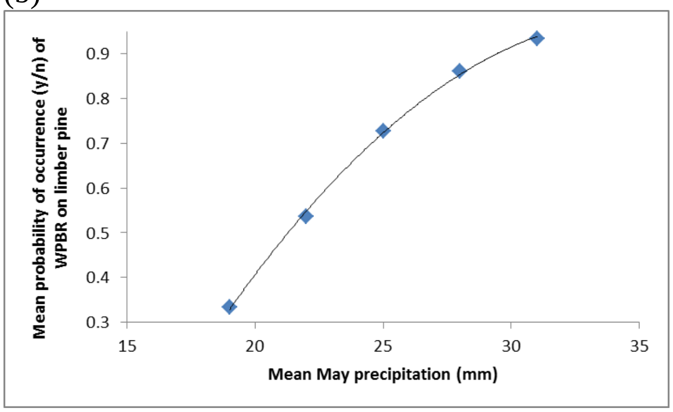


Figure 1.6: Logistic regression analysis predicting occurrence (y/n) of WPBR on limber pine on a subplot using variables selected in the final model (fit using PROC GLIMMIX with study area as a random effect, in SAS) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Relationship with response variable was plotted using the 5th, 25th, 50th, 75th, and 95th percentiles of the variable of interest and mean values for the other variables. Predicted values were back transformed. Positive relationships exist between (a) occurrence of WPBR and stems/ha of limber pine and (b) mean May precipitation (mm).

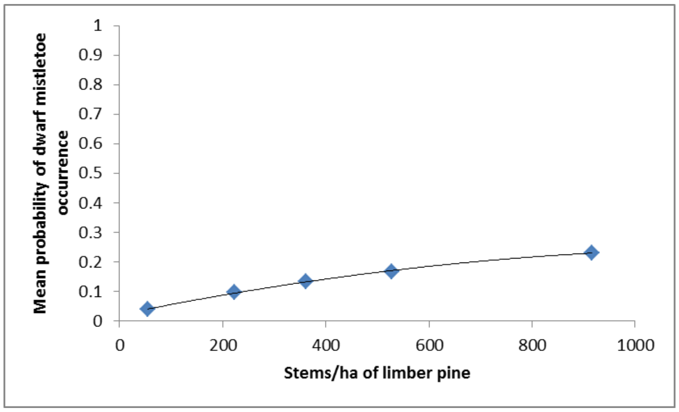


Figure 1.7: Logistic regression analysis predicting occurrence (y/n) of dwarf mistletoe on limber pine on a subplot using variables selected in the final model (fit using PROC GLIMMIX with /s dist=binary and study area as a random effect, in SAS) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012 Relationship with response variable was plotted using the 5th, 25th, 50th, 75th, and 95th percentiles of the variable of interest and mean values for the other variables. Predicted values were back transformed. Positive relationships exist between occurrence of dwarf mistletoe and stems/ha of limber pine.

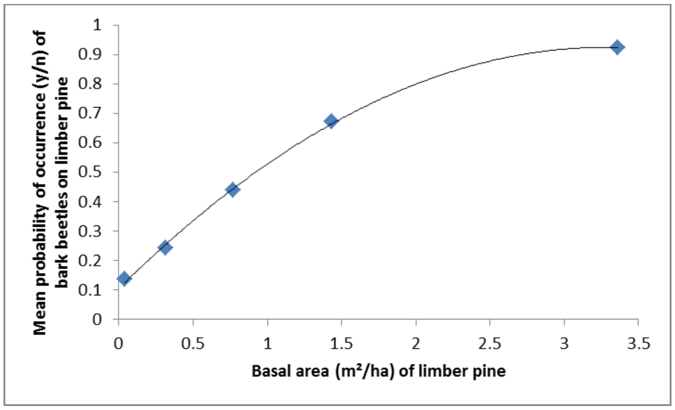


Figure 1.8: Logistic regression analysis predicting occurrence (y/n) of bark beetles on limber pine on a subplot using variables selected in the final (fit using PROC GLIMMIX with /s dist=binary and study area as a random effect, in SAS) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Relationship with response variable was plotted using the 5th, 25th, 50th, 75th, and 95th percentiles of the variable of interest and mean values for the other variables. Predicted values were back transformed. A positive relationship exists between occurrence of bark beetles on limber pine on a subplot and basal area (m^2/ha) of limber pine.

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Appendix I: Additional Tables and Figures

Table 1.6: Plot summary data from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

		Slope (%)				Aspect[2] (% of plots)				Elevation (m)				Slope position (% of plots)						Stand structure (% of plots)				Disturbance history (% of plots)			
State, geographic range, and study area	n[1]	mean	std	min	max	east	south	west	north	mean	std	min	max	backslope	footslope	shoulder	summit	toeslope	valley bottom	CM[3]	CMO[4]	MM[5]	OP[6]	tree cutting	fire	other human disturbance	grazing
Colorado																											
Front Range																											
Boulder County	14	16	9	3	33	16	20	27	38	2735	117	2568	2947	31	14	43	5	-	7	7	33	45	14	38	-	34	7
North	25	16	11	3	37	20	24	37	19	2669	147	2484	3129	39	11	31	12	5	3	-	33	1	65	33	23	4	52
Wyoming																											
Laramie Mtns																											
Pole Mtn	24	12	8	3	33	8	11	33	47	2544	80	2440	2700	18	13	53	10	6	1	-	19	8	72	10	7	17	88
East	24	18	9	6	46	13	15	15	58	2347	83	2116	2456	36	19	24	8	8	4	8	11	44	36	-	2	13	40
West	24	19	8	4	33	23	25	16	36	2482	110	2326	2717	39	13	26	13	-	10	11	8	26	54	-	-	6	42
Muddy Mtn	21	17	14	3	62	10	19	26	45	2339	150	1969	2521	37	11	33	17	-	2	2	10	17	71	2	4	24	40
Medicine Bow Mtns																											
South	24	11	8	2	30	17	24	28	32	2633	140	2398	2907	7	6	44	36	6	1	-	38	1	61	17	11	3	67
North	24	19	10	6	39	22	28	38	13	2797	176	2490	3084	29	-	49	22	-	-	24	11	-	65	6	19	7	13
Sierra Madre	24	17	8	6	36	13	36	33	18	2736	119	2459	2937	29	1	44	14	7	4	-	24	4	72	11	18	4	71
Sweetwater Basin																											
Shirley Mtns	24	15	8	2	33	19	28	32	21	2424	117	2241	2690	24	13	33	11	14	6	-	14	3	83	-	4	-	88
Ferris Mtns	6	18	10	10	34	-	28	39	33	2293	81	2157	2381	17	33	28	6	6	11	-	-	-	100	-	-	-	100
Green Mtns	24	18	13	1	54	22	31	26	21	2516	244	2177	3269	39	11	28	22	-	-	1	11	6	82	15	6	-	90
Beaver Divide	16	21	13	3	49	23	13	14	50	2287	143	2060	2491	42	21	21	13	-	4	-	-	23	77	-	-	13	66
Wind River Range																											
South	27	14	9	5	45	16	36	12	36	2599	117	2348	2911	38	14	37	10	1	-	2	-	37	60	12	3	8	56
Reservation	18	27	11	11	44	22	26	15	36	2654	170	2320	2915	59	13	24	2	-	2	-	-	28	72	6	11	10	67
North	28	24	15	4	66	16	28	21	36	2503	115	2328	2719	52	5	30	10	2	1	6	2	48	44	10	6	1	56
Absaroka Range																											
South	21	28	16	3	64	26	30	15	29	2462	231	1763	2690	68	5	10	10	-	8	-	19	38	43	1	17	11	29
Shoshone Canyon	16	23	14	5	52	25	19	5	52	2083	367	1594	2680	46	17	23	8	4	2	-	6	10	83	11	5	6	38
North	24	23	14	3	60	18	24	20	39	2054	184	1799	2550	54	18	8	14	6	-	-	4	35	61	5	1	14	56
Bighorn Basin	11	25	21	5	64	2	18	30	50	1918	284	1558	2389	30	6	33	15	12	3	6	-	24	70	7	-	7	52
Bighorn Mtns																											
East	17	22	10	6	41	18	24	16	43	2404	131	1941	2512	61	29	8	-	2	-	10	-	39	51	4	4	-	57
South	20	22	9	6	40	15	26	26	33	2518	227	2069	2819	55	12	10	20	3	-	-	10	27	63	3	3	5	49
North	24	25	12	6	67	18	32	17	33	2478	240	2013	2855	63	3	21	14	-	-	-	1	32	67	1	5	7	58
Montana																											
Pryor Mtns	20	18	10	7	43	13	24	26	38	2076	377	1493	2601	47	13	15	15	10	-	5	3	32	60	4	-	16	49
Terry Badlands	8	15	9	5	24	13	16	22	50	858	15	835	874	29	17	38	13	4	-	-	-	42	58	-	-	6	75
	508	19				17	24	24	36	2376				40	13	29	13	6	4	7	14	25	64	10	8	10	56

[1]One plot = three 60 x 6 m subplots placed at random bearings with a 30 x 6 m WPBR alternate host plot at the end of each subplot.
[2]Aspect: east ≥ 45 and < 135 degrees, south ≥ 135 and < 225 degrees, west ≥ 225 and < 315 degrees, north ≥ 315 and < 45 degrees.
[3]Closed canopy multistory.
[4]Closed canopy multistory with open individuals and/or open scattered clumps.
[5]Closed canopy single story with open individuals and/or open scattered clumps (includes mosaic of closed canopy single and multistory).
[6]Open canopy, scattered individuals and/or scattered clumps.

Table 1.7: Limber pine tree summary data from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

							crown class																			
State, geographic		mean #	crown dieback (%)				codominant				dominant				intermediate				open				overtopped			
range, and study area	n[1]	trees	mean	std	min	max	mean	std	min	max	mean	std	min	max	mean	std	min	max	mean	std	min	max	mean	std	min	max
Colorado																										
Front Range																										
Boulder County	14	47	8	9	0	30	37	13	11	55	3	1	1	5	40	15	11	65	16	21	2	78	9	5	3	19
North	24	35	6	5	0	17	30	17	4	77	5	3	2	9	53	21	16	100	16	11	1	49	11	8	3	36
Wyoming																										
Laramie Mtns																										
Pole Mtn	24	33	11	5	3	22	24	14	3	50	4	1	3	5	56	19	8	88	17	14	4	46	10	7	3	26
East	24	34	7	5	0	17	32	10	15	48	7	5	3	14	43	20	4	71	17	15	3	59	16	10	4	34
West	24	27	2	3	0	14	30	17	5	76	7	2	5	13	30	15	4	60	39	28	3	100	10	9	4	38
Muddy Mtn	21	32	6	5	0	18	27	20	3	77	5	4	2	13	24	12	6	45	54	28	7	100	10	6	2	21
Medicine Bow Mtns																										
South	24	27	6	11	0	49	21	11	3	41	4	2	2	7	50	22	8	89	25	21	2	67	11	8	3	35
North	24	29	7	7	0	25	20	11	6	46	3	1	2	4	59	16	36	88	18	13	4	48	9	5	4	22
Sierra Madre	24	28	2	4	0	19	17	11	3	38	5	2	3	8	59	20	6	100	25	15	1	63	8	4	3	18
Sweetwater Basin																										
Shirley Mtns	24	46	8	7	1	27	25	15	3	57	6	5	2	14	49	18	8	84	20	11	4	43	6	3	2	12
Ferris Mtns	6	28	8	9	0	21	23	12	3	41	6	4	4	11	34	15	7	53	32	14	7	46	10	4	6	14
Green Mtns	24	51	11	11	1	53	14	5	5	24	2	1	1	3	56	14	29	88	19	12	1	41	12	9	2	36
Beaver Divide	16	40	8	10	0	32	20	13	3	40	4	2	3	6	36	24	14	93	54	25	8	93	7	5	2	21
Wind River Range																										
South	27	32	6	5	0	18	31	16	6	63	4	1	2	4	29	12	6	58	45	31	3	100	8	5	1	24
Reservation	17	24	11	7	0	28	26	10	13	39	4	2	2	6	28	18	3	60	57	29	17	100	14	11	2	40
North	28	28	3	2	0	9	34	20	7	67	1	-	1	1	36	22	4	81	40	34	3	100	14	12	3	36
Absaroka Range																										
South	21	27	18	10	1	36	33	20	8	61	5	3	3	9	37	24	6	83	37	29	6	100	7	5	2	19
Shoshone Canyon	16	31	8	7	0	25	11	10	4	38	-	-	-	-	58	24	10	93	44	30	16	100	5	2	2	8
North	24	29	11	16	0	61	44	26	6	86	7	4	4	11	31	29	3	94	41	33	4	100	6	4	2	17
Bighorn Basin	11	35	7	5	0	16	36	28	6	75	3	1	2	4	23	25	2	65	56	38	3	100	7	3	2	12
Bighorn Mtns																										
East	17	35	11	8	3	29	34	18	14	69	14	9	7	20	31	22	5	80	34	21	2	71	11	5	2	20
South	20	31	11	6	4	24	33	19	4	70	9	5	6	13	39	26	7	88	28	24	4	88	12	5	4	22
North	24	38	6	5	0	25	46	20	4	76	10	11	2	18	27	23	5	95	29	18	5	64	6	4	2	15
Montana																										
Pryor Mtns	20	36	7	6	0	19	43	24	4	76	4	0	4	4	17	12	2	42	55	37	4	100	9	6	3	25
Terry Badlands	8	54	5	4	0	11	40	14	17	56	3	-	3	3	22	10	13	41	30	14	15	56	9	5	3	18
	506	34	8				29				5				39				34				9			

[1]One plot = three 60 x 6 m subplots placed at random bearings with a 30 x 6 m WPBR alternate host plot at the end of each subplot.

Table 1.8: A comparison of health status of limber pine at the stand level in 2002 - 2004 (Kearns and Jacobi 2007) and a monitoring study of limber pine stands in 2011 - 2012 at 13 study areas in Colorado and Wyoming.

State, geographic range, and study area	Year	n[1, 2]	Health status					
			healthy[3]	p-value	declining[4]	p-value	dead[5]	p-value
Colorado								
Front Range								
North	2003	75	85.56	0.0136	10.3	0.1053	4.1	0.0212
	2011	24	74		16		11	
Wyoming								
Laramie Mtns								
Pole Mtn	2002	93	82	<0.0001	15	<0.0001	3	0.0002
	2011	24	55		27		18	
East	2002	29	73	0.0029	16	0.0508	11	0.0106
	2012	24	56		23		21	
West	2002	30	87	0.0056	7	0.0500	5	0.0510
	2012	24	75		12		13	
Muddy Mtn	2003	20	81	<0.0001	16	0.0016	4	0.0340
	2012	21	55		33		12	
Medicine Bow Mtns								
South	2002, 2003	69	80	0.0003	14	0.6371	6	<0.0001
	2011	24	57		16		27	
North	2002, 2003	60	85	<0.0001	10	0.0118	6	<0.0001
	2011	24	43		19		38	
Sierra Madre	2002, 2003	31	86	0.0002	8	0.0110	6	<0.0001
	2011	24	63		3		33	
Sweetwater Basin								
Shirley Mtns	2002	33	80	0.0007	15	0.0039	5	0.0069
	2011	24	59		28		13	
Ferris Mtns	2003	7	64	0.6221	29	0.8948	7	0.3083
	2011	6	54		31		15	
Green Mtns	2002	22	83	<0.0001	14	0.0004	4	0.0040
	2011	24	49		34		18	
Wind River Range								
Reservation	2004	15	59	<0.0001	35	0.9935	6	<0.0001
	2012	18	18		35		47	
Absaroka Range								
South	2003	20	93	<0.0001	5	<0.0001	2	<0.0001
	2012	20	16		44		40	
	2002-2004		80		15		5	
	2011-2012		52		25		23	

[1]2002 – 2004 (Kearns and Jacobi 2007): one plot = 2 - 5 transects each 61 x 4.6 m, placed at random bearings with a 30.5 x 4.6 m *Ribes* transect at the end of each main transect.

[2]2011 – 2012: one plot = three 60 x 6 meter subplots placed at random bearings with a 30 x 6 meter WPBR alternate host subplot at the end of each main subplot.
[3]Percent of stems with health status = 1, no visual damage to crown or stem up to 5% damage.
[4]Percent of stems with health status = 2, declining, 6-50% of crown showing symptoms that indicates it is dead or will be or health status = 3, dying, >50% of crown showing symptoms or is damaged.
[5]Percent of stems with health status = 4, recent dead, no green needles, red needles but fines still present, health status = 5, old dead, no fine twigs, no needles, >50% bark still present, or health status = 6, very old dead, no fine twigs, no needles, <50% of bark present.

Table 1.9: A comparison of occurrence and incidence of live and dead limber pine at the stand level in 2002 - 2004 (Kearns and Jacobi 2007) and a monitoring study of limber pine stands in 2011 - 2012 at 12 study areas in Colorado and Wyoming.

State, geographic range, and study area	Year	n[1, 2]	WPBR				Bark beetles				Dwarf mistletoe			
			% plots	p-value	% stems	p-value	% plots	p-value	% stems	p-value	% plots	p-value	% stems	p-value
Colorado														
Front Range														
North	2003	75	26.7	0.0066	4.08	0.1062	12	<0.0001	0.7	0.0010	28.0	0.6155	8.4	0.7675
	2011	24	58		8.0		71		14		33		7.0	
Wyoming														
Laramie Mtns														
Pole Mtn	2002	93	91	0.2038	30.1	0.4006	3	<0.0001	0	0.0002	15	1.0000	2.9	0.7199
	2011	24	100		34.2		88		14.8		13		4.0	
East	2002	29	97	0.5841	26.1	0.1820	17	<0.0001	1	0.0029	24	0.7351	9.3	0.4056
	2012	24	92		19.5		75		7		17		4.8	
West	2002	30	60	0.7837	6.4	0.3677	20	0.2228	1	0.0922	13	0.3111	1.4	0.1130
	2012	24	54		8.9		38		6		25		7.5	
Muddy Mtn	2003	20	100	0.4878	37.1	0.8008	15	0.2772	1	0.0964	10	1.0000	3.4	0.2299
	2012	21	95		35.4		33		6		10		0.3	
Medicine Bow Mtns														
South	2002, 2003	69	7	0.0304	0.9	0.1822	29	<0.0001	2	<0.0001	58	1.0000	22.4	0.9793
	2011	24	25		3.4		96		23		58		22.6	
North	2002, 2003	60	22	0.5719	1.2	0.1060	8	<0.0001	0	<0.0001	33	0.0491	10.8	0.1033
	2011	24	29		2.6		96		35		58		20.5	
Sierra Madre	2002, 2003	31	0	1.0000	0.0		35	0.0023	2	<0.0001	13	0.1234	1.8	0.1177
	2011	24	0		0.0		79		31		0		0.0	
Sweetwater Basin														
Shirley Mtns	2002	33	91	0.2556	19.3	0.0001	24	<0.0001	1	0.0003	27	0.0285	9.7	0.9939
	2011	24	100		38.9		79		10		58		9.8	
Ferris Mtns	2003	7	57	1.0000	22.7	0.9711	57	0.5594	1	0.0987	57	1.0000	22.8	0.9209
	2011	6	50		23.3		83		12		67		20.7	
Green Mtns	2002	22	100	1.0000	35.7	0.4783	9	<0.0001	0	0.0016	27	0.1405	5.4	0.1833
	2011	24	100		40.2		83		13		50		15.3	
Wind River Range														
Reservation	2004	15	100	1.0000	55.8	0.6521	20	<0.0001	1	<0.0001	27	0.4719	9.4	0.6161
	2012	18	100		52.1		89		29		41		13.5	
Absaroka Range														
South	2003	20	95	1.0000	18.6	<0.0001	0	<0.0001	0	<0.0001	0	1.0000	0.0	0.3299
	2012	20	100		72.2		90		31		5		2.3	
	2002-2004		65		20		19		1		26		8	
	2011-2012		69		26		77		18		33		10	

[1]2002 – 2004 (Kearns and Jacobi 2007): one plot = 2 - 5 transects each 61 x 4.6 m, placed at random bearings with a 30.5 x 4.6 m *Ribes* transect at the end of each main transect.
[2]2011 – 2012: one plot = three 60 x 6 meter subplots placed at random bearings with a 30 x 6 meter WPBR alternate host subplot at the end of each main subplot.

Table 1.10: Canker data from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012. Cankers/tree is of limber pines infected with WPBR.

State, geographic range, and study area	Cankers/tree				Cankers/ha				Number of cankers per size class (cm) per infected live limber pine x 1000									
	mean	std	min	max	mean	std	min	max	0-12	>12-24	>24-36	>36-48	>48-60	>60-72	>72-84	>84-96	>96-108	>108
Colorado																		
Front Range																		
Boulder County	0.0	0.1	0.0	0.5	2	7	0	28	500	500	0	0	0	0	0	0	0	0
North	1.0	1.4	0.0	6.0	53	93	0	333	1250	729	375	125	21	21	21	0	0	0
Wyoming																		
Laramie Mtns																		
Pole Mtn	4.0	2.9	0.5	13.6	517	471	28	1704	754	873	795	496	295	209	134	101	15	194
East	1.5	1.1	0.0	3.9	124	112	0	333	291	440	291	172	112	45	22	7	0	0
West	0.5	0.7	0.0	3.0	30	41	0	120	311	400	467	200	67	22	22	0	0	0
Muddy Mtn	5.0	4.4	0.7	17.0	629	758	65	3324	906	1075	953	518	200	129	51	16	8	0
Medicine Bow Mtns																		
South	0.3	0.8	0.0	3.4	27	84	0	380	550	1050	500	500	150	100	0	100	0	0
North	0.4	0.9	0.0	3.0	25	57	0	231	423	731	538	423	115	0	0	0	0	38
Sierra Madre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sweetwater Basin																		
Shirley Mtns	3.7	1.9	1.2	9.4	685	613	176	3083	915	1044	887	424	213	44	46	36	13	64
Ferris Mtns	6.1	7.5	0.0	18.0	685	904	0	2065	1486	2162	1757	676	405	54	0	0	0	54
Green Mtns	5.0	2.6	1.3	12.3	983	749	37	2963	1248	1386	866	329	178	81	38	21	6	28
Beaver Divide	3.3	3.4	0.0	12.3	500	593	0	1833	1915	1201	476	146	37	6	6	0	0	0
Wind River Range																		
South	3.0	3.4	0.0	11.0	400	628	0	2231	1258	1949	882	185	22	6	0	0	0	0
Reservation	6.9	7.4	0.7	31.1	822	761	19	2565	2069	1250	667	241	79	32	14	0	0	0
North	1.5	1.2	0.0	4.3	155	164	0	685	966	701	339	75	52	17	0	11	0	0
Absaroka Range																		
South	5.4	2.5	1.2	10.5	941	763	93	3380	1797	1489	657	206	40	11	0	3	0	0
Shoshone Canyon	0.8	1.3	0.0	4.3	107	193	0	694	781	797	656	219	94	16	0	0	0	0
North	2.6	2.4	0.0	11.0	299	308	0	880	862	966	552	217	64	30	0	0	0	0
Bighorn Basin	2.1	1.8	0.0	5.0	287	289	0	769	804	784	773	299	124	62	10	21	0	10
Bighorn Mtns																		
East	4.8	2.2	2.8	10.3	758	739	167	2731	847	1200	1012	463	125	35	12	8	0	4
South	4.0	1.4	1.6	6.6	520	354	93	1514	621	799	810	413	204	52	15	15	0	4
North	2.1	1.6	0.0	6.4	337	445	0	1819	867	931	508	222	69	16	0	4	0	0
Montana																		
Pryor Mtns	2.8	2.5	0.0	9.7	390	390	0	1139	696	991	871	313	166	37	0	5	0	0
Terry Badlands	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 1.11: Site (plot), ground cover, and WPBR alternate host variables used during statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

	Site (plot) variables	**Ground cover variables**	**WPBR alternate host variables**
	Northing (latituide)	Soil (percent cover)	Stream density within 1 km
	Elevation (m)	Litter (percent cover)	Area (m^2) occupied by *Ribes* spp.
Aspect	North	Rock (percent cover)	Area (m^2) occupied by *Castilleja* spp.
	South	Tree/log (percent cover)	
	East	Lichens/moss (percent cover)	
	West	Grass (percent cover)	
	Slope (percent)	Forbs (percent cover)	
Slope position	Summit	Shrubs (percent cover)	
	Shoulder	Common juniper (percent of shrub cover)	
	Backslope (includes footslope and toeslope)	Kinnikinnick (percent of shrub cover)	
	Valley bottom	Fringed sagebrush (percent of shrub cover)	
Stand structure	Closed canopy multistory	Big sagebrush (percent of shrub cover)	
	Closed canopy multistory with open individuals and/or open scattered clumps	Bog birch (percent of shrub cover)	
		Mountain mahogany (percent of shrub cover)	
	Closed canopy single story with open individuals and/or open scattered clumps	Service berry (percent of shrub cover)	
		Shrubby cinquefoil (percent of shrub cover)	
	Open canopy, scattered individuals and/or scattered clumps	Bitterbrush (percent of shrub cover)	
		Skunkbush (percent of shrub cover)	
Disturbance history	Site preparation (tillage)	Rabbitbrush (percent of shrub cover)	
	Artificial regeneration	False rasberry (percent of shrub cover)	
	Natural regeneration (after disturbance)	Wild red rasberry (percent of shrub cover)	
	Stand improvement	Rose (percent of shrub cover)	
	Tree cutting	*Ribes cereum* (percent of shrub cover)	
	Fire	*Ribes inerme* (percent of shrub cover)	
	Other silvicultural treatments	*Vaccinium* spp. (percent of shrub cover)	
	Other human disturbance	Dogwood (percent of shrub cover)	
	Natural disturbance	Snowberry (percent of shrub cover)	
	Land clearing		
	Animal damage		
	Type conversion		
	Mining		
	Grazing		
Total	29	27	3

Table 1.12: Seedling and stand (tree) variables used in statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

Seedling variables	**Stand (tree) variables**
Limber pine seedling height (cm)	Presence of beetles in limber pine
Average terminal growth (mm) of the previous 2 years	Presence of dwarf mistletoe in limber pine
sqrt proportion of limber pine seedlings with wpbr	Presence of wpbr in limber pine
$\log_{10}$ stems/ha of limber pine seedlings	Percent limber pine with bark beetles
$\log_{10}$ stems/ha of all other seedlings	Percent limber pine with dwarf mistletoe
$\log_{10}$ stems/ha of other pine seedlings	Percent limber pine with wpbr
$\log_{10}$ stems/ha of aspen seedlings	Proportion of limber pine with dbh < 5 cm
$\log_{10}$ stems/ha of spruce-fir seedlings	Proportion of limber pine with dbh > 5 - 10 cm
$\log_{10}$ stems/ha of all seedlings	Proportion of limber pine with dbh > 10 - 20 cm
Limber pine seedling presence on a subplot	Proportion of limber pine with dbh >20 cm
Presence of wpbr on a limber pine seedling	Proportion of limber pine in the codominant (includes dominant) crown class
Presence of dwarf mistletoe on a limber pine seedling	Proportion of limber pine in the intermediate crown class
Dead top on limber pine seedlings	Proportion of limber pine in the open-grown crown class
Forbs as dominant groundcover next to seedling	Proportion of limber pine in the overtopped
Grass as dominant groundcover next to seedling	Crown dieback (percent)
Lichens/moss as dominant groundcover next to seedling	$\log_{10}$ stems/ha of limber pine
Litter as dominant groundcover next to seedling	$\log_{10}$ basal area (m^2/ha) of limber pines
Rock as dominant groundcover next to seedling	$\log_{10}$ basal area (m^2/ha) of limber pines with bark beetles
Shrubs as dominant groundcover next to seedling	$\log_{10}$ basal area (m^2/ha) of limber pines with dwarf mistletoe
Soil as dominant groundcover next to seedling	$\log_{10}$ basal area (m^2/ha) of limber pines with wpbr
Tree/log as dominant groundcover next to seedling	$\log_{10}$ basal area (m^2/ha) of limber pines with bark beetles and dwarf mistletoe
Log as a seedling microsite object	$\log_{10}$ stems/ha of other pines
Rock as a seedling microsite object	$\log_{10}$ basal area (m^2/ha) of other pines
Shrub as seedling microsite object	$\log_{10}$ basal area (m^2/ha) of other pines with bark beetles
Stump as a seedling microsite object	$\log_{10}$ basal area (m^2/ha) of other pines with dwarf mistletoe
Tree/log as a seedling microsite object	$\log_{10}$ stems/ha of all pines
	$\log_{10}$ basal area (m^2/ha) of all pines
	$\log_{10}$ basal area (m^2/ha) of all pines with bark beetles
	$\log_{10}$ basal area (m^2/ha) of all pines with dwarf mistletoe
	$\log_{10}$ stems/ha of all other species
	$\log_{10}$ basal area (m^2/ha) of all other species
	$\log_{10}$ stems/ha all live trees
	$\log_{10}$ basal area (m^2/ha) all live trees
	$\log_{10}$ dbh of all live trees
	$\log_{10}$ stems/ha of aspen
	$\log_{10}$ basal area (m^2/ha) of aspen
	$\log_{10}$ stems/ha of spruce-fir
	$\log_{10}$ basal area (m^2/ha) of spruce-fir
	$\log_{10}$ stems/ha of spruce-fir
	$\log_{10}$ tree cankers/ha
	proportion of basal area (m^2/ha) of limber pine trees
	$\log_{10}$ stems/ha all trees
	$\log_{10}$ basal area (m^2/ha) all trees
	$\log_{10}$ stems/ha all dead trees
	$\log_{10}$ basal area (m^2/ha) all dead trees
	$\log_{10}$ dbh of all dead trees
Total: 26	Total: 46

Table 1.13: Meteorological variables obtained from the PRISM dataset (Daly et al. 2002) provided by FHTET (USDA FS Forest Health Technology Enterprise Team, Fort Collins, CO) used in statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

240 m data		30 m data
12 month moderate or greater drought frequency	Average minimum temperature in July - September	Growing season precipitation (mm)
36 month moderate or greater drought frequency	Average maximum temperature in the warmest month	Annual precipitation (mm)
60 month moderate or greater drought frequency	Average maximum temperature for year	Mean annual temperature - tenths of degrees C
Autumn frost date	Average maximum temperature in January	Maximum temperature in the warmest month - tenths of degrees C
Spring frost day	Average maximum temperature in February	Minimum temperature in the coldest month - tenths of degrees C
Frost free period	Average maximum temperature in March	Average temperature in the coldest month - tenths of degrees C
Growing degree days	Average maximum temperature in April	Average temperature in the warmest month - tenths of degrees C
Three-year (2006 - 2008) standardized moisture difference z-score	Average maximum temperature in May	1st principle component monthly precipitation
Three-year (2007 - 2009) standardized moisture difference z-score	Average maximum temperature in June	2nd principle compoent monthly precipitation
Five-year (2004 - 2008) standardized moisture difference z-score	Average maximum temperature in July	Ratio of growing season precip to annual precip - No units (index)
Five-year (2005 - 2009) standardized moisture difference z-score	Average maximum temperature in August	Seasonal moisture index, the ratio of degree-days >5 °C
growing season precipitation (mm)	Average maximum temperature in September	accumulating within the frost-free period to seasonal precipitation
Annual moisture index: the ratio of degree-days > 5 degrees	Average maximum temperature in October	Direct short-wave radiation
celsius to annual precipitation in millimeters.	Average maximum temperature in November	Diffuse short-wave radiation
Mean annual ppt	Average maximum temperature in December	Derived short-wave radiation
Mean January precipitation (mm)	Average maximum temperature in May - June	Short-wave radiation
Mean February precipitation (mm)	Average maximum temperature in July - September	1st principle component average temperature
Mean March precipitation (mm)	Average temperature in the warmest month	1st principle component maximum temperature
Mean April precipitation (mm)	Average temperature for year (mean annual temp)	1st principle component minimum temperature
Mean May precipitation (mm)	Average temperature in January	2nd principle compoent minimum temperature
Mean June precipitation (mm)	Average temperature in February	Water vapor pressure
Mean July precipitation (mm)	Average temperature in March	Soil component dominance
Mean August precipitation (mm)	Average temperature in April	Soil component frequency
Mean September precipitation (mm)	Average temperature in May	Julian date when the sum of degree-days >5 °C reaches 100 - Date
Mean October precipitation (mm)	Average temperature in June	Degree-days <0 °C - degree days
Mean November precipitation (mm)	Average temperature in July	Degree-days >5 °C - degree days
Mean December precipitation (mm)	Average temperature in August	Soil drainage index - derived from SSURGO/STATSGO/NFS
Mean May - June precipitation (mm)	Average temperature in September	Soil data source - SSURGO/STATSGO/USFS
Mean July - September precipitation (mm)	Average temperature in October	Frost-free days - # Days
Ratio GS ppt : Mean annual ppt	Average temperature in November	Julian date of the first freezing date of autumn - Date
Seasonal moisture index, the ratio of degree-days >5 °C	Average temperature in December	Length of the frost-free period - # Days
accumulating within the frost-free period to seasonal precipitation	Average temperature in May - June	Fertility index - derived from SSURGO/STATSGO/NFS
Short wave radiation	Average temperature in July - September	Growing-degree days
Average temperature in the coldest month	Water vapor pressure	Degree-days >5 °C accumulating within the frost-free period
Average minimum temperature in the coldest month	Annual average relative humidity	Julian date of the last freezing date of spring - Date
Average minimum temperature in January	Average relative humidity in January	Topographic Relative Moisture Index
Average minimum temperature in February	Average relative humidity in February	Topographic Relative Moisture Index - Modified
Average minimum temperature in March	Average relative humidity in March	Topographic scale
Average minimum temperature in April	Average relative humidity in April	
Average minimum temperature in May	Average relative humidity in May	
Average minimum temperature in June	Average relative humidity in June	
Average minimum temperature in July	Average relative humidity in July	
Average minimum temperature in August	Average relative humidity in August	
Average minimum temperature in September	Average relative humidity in September	
Average minimum temperature in October	Average relative humidity in October	
Average minimum temperature in November	Average relative humidity in November	
Average minimum temperature in December	Average relative humidity in December	
Average minimum temperature in May - June	Average relative humidity in May - June	
	Average relative humidity in July - September	
	Total: 133	

Table 1.14: Meteorological variables extracted from Daymet Daily Surface Gridded Data used in statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

Total precipitation (mm) 2007-2010	Average relative humdity in January 2007	Total precipitation (mm) in January 2007	Maximum temperature in January 2007	Minimum temperature in January 2007
May precipitation (mm) 2007-2010	Average relative humdity in February 2007	Total precipitation (mm) in February 2007	Maximum temperature in February 2007	Minimum temperature in February 2007
May-June precipitation (mm) 2007-2010	Average relative humdity in March 2007	Total precipitation (mm) in March 2007	Maximum temperature in March 2007	Minimum temperature in March 2007
July-September precipitation (mm) 2007-2010	Average relative humdity in April 2007	Total precipitation (mm) in April 2007	Maximum temperature in April 2007	Minimum temperature in April 2007
Average relative humidty 2007-2010	Average relative humdity in May 2007	Total precipitation (mm) in May 2007	Maximum temperature in May 2007	Minimum temperature in May 2007
May relative humidty 2007-2010	Average relative humdity in June 2007	Total precipitation (mm) in June 2007	Maximum temperature in June 2007	Minimum temperature in June 2007
May-June relative humidity 2007-2010	Average relative humdity in July 2007	Total precipitation (mm) in July 2007	Maximum temperature in July 2007	Minimum temperature in July 2007
July-September relative humidty 2007-2010	Average relative humdity in August 2007	Total precipitation (mm) in August 2007	Maximum temperature in August 2007	Minimum temperature in August 2007
Average maximum temperature 2007-2010	Average relative humdity in September 2007	Total precipitation (mm) in September 2007	Maximum temperature in September 2007	Minimum temperature in September 2007
May maximum temperature 2007-2010	Average relative humdity in October 2007	Total precipitation (mm) in October 2007	Maximum temperature in October 2007	Minimum temperature in October 2007
May-June maximum temperature 2007-2010	Average relative humdity in November 2007	Total precipitation (mm) in November 2007	Maximum temperature in November 2007	Minimum temperature in November 2007
July-September maximum temperature 2007-2010	Average relative humdity in December 2007	Total precipitation (mm) in December 2007	Maximum temperature in December 2007	Minimum temperature in December 2007
Average minimum temperature 2007-2010	Average relative humdity in January 2008	Total precipitation (mm) in January 2008	Maximum temperature in January 2008	Minimum temperature in January 2008
May minimum temperature 2007-2010	Average relative humdity in February 2008	Total precipitation (mm) in February 2008	Maximum temperature in February 2008	Minimum temperature in February 2008
May-June minimum temperature 2007-2010	Average relative humdity in March 2008	Total precipitation (mm) in March 2008	Maximum temperature in March 2008	Minimum temperature in March 2008
July-September minimum temperature 2007-2010	Average relative humdity in April 2008	Total precipitation (mm) in April 2008	Maximum temperature in April 2008	Minimum temperature in April 2008
Total precipitation (mm) 2010-2011	Average relative humdity in May 2008	Total precipitation (mm) in May 2008	Maximum temperature in May 2008	Minimum temperature in May 2008
Total precipitation (mm) 2009-2010	Average relative humdity in June 2008	Total precipitation (mm) in June 2008	Maximum temperature in June 2008	Minimum temperature in June 2008
May-September total precipitation 2010-2011	Average relative humdity in July 2008	Total precipitation (mm) in July 2008	Maximum temperature in July 2008	Minimum temperature in July 2008
May-September total precipitation 2009-2010	Average relative humdity in August 2008	Total precipitation (mm) in August 2008	Maximum temperature in August 2008	Minimum temperature in August 2008
October-April total precipitation 2010-2011	Average relative humdity in September 2008	Total precipitation (mm) in September 2008	Maximum temperature in September 2008	Minimum temperature in September 2008
October-April total precipitation 2009-2010	Average relative humdity in October 2008	Total precipitation (mm) in October 2008	Maximum temperature in October 2008	Minimum temperature in October 2008
May-September maximum temperature 2010-2011	Average relative humdity in November 2008	Total precipitation (mm) in November 2008	Maximum temperature in November 2008	Minimum temperature in November 2008
May-September maximum temperature 2009-2010	Average relative humdity in December 2008	Total precipitation (mm) in December 2008	Maximum temperature in December 2008	Minimum temperature in December 2008
May-June maximum temperature 2010-2011	Average relative humdity in January 2009	Total precipitation (mm) in January 2009	Maximum temperature in January 2009	Minimum temperature in January 2009
May-June maximum temperature 2009-2010	Average relative humdity in February 2009	Total precipitation (mm) in February 2009	Maximum temperature in February 2009	Minimum temperature in February 2009
July-September maximum temperature 2010-2011	Average relative humdity in March 2009	Total precipitation (mm) in March 2009	Maximum temperature in March 2009	Minimum temperature in March 2009
July-September maximum temperature 2009-2010	Average relative humdity in April 2009	Total precipitation (mm) in April 2009	Maximum temperature in April 2009	Minimum temperature in April 2009
May-September minimum temperature 2010-2011	Average relative humdity in May 2009	Total precipitation (mm) in May 2009	Maximum temperature in May 2009	Minimum temperature in May 2009
May-September minimum temperature 2009-2010	Average relative humdity in June 2009	Total precipitation (mm) in June 2009	Maximum temperature in June 2009	Minimum temperature in June 2009
May-June minimum temperature 2010-2011	Average relative humdity in July 2009	Total precipitation (mm) in July 2009	Maximum temperature in July 2009	Minimum temperature in July 2009
May-June minimum temperature 2009-2010	Average relative humdity in August 2009	Total precipitation (mm) in August 2009	Maximum temperature in August 2009	Minimum temperature in August 2009
July-September minimum temperature 2010-2011	Average relative humdity in September 2009	Total precipitation (mm) in September 2009	Maximum temperature in September 2009	Minimum temperature in September 2009
July-September minimum temperature 2009-2010	Average relative humdity in October 2009	Total precipitation (mm) in October 2009	Maximum temperature in October 2009	Minimum temperature in October 2009
Average relative humidity in 2000	Average relative humdity in November 2009	Total precipitation (mm) in November 2009	Maximum temperature in November 2009	Minimum temperature in November 2009
Average relative humidity in 2001	Average relative humdity in December 2009	Total precipitation (mm) in December 2009	Maximum temperature in December 2009	Minimum temperature in December 2009
Average relative humidity in 2002	Average relative humdity in January 2010	Total precipitation (mm) in January 2010	Maximum temperature in January 2010	Minimum temperature in January 2010
Average relative humidity in 2003	Average relative humdity in February 2010	Total precipitation (mm) in February 2010	Maximum temperature in February 2010	Minimum temperature in February 2010
Average relative humidity in 2004	Average relative humdity in March 2010	Total precipitation (mm) in March 2010	Maximum temperature in March 2010	Minimum temperature in March 2010
Average relative humidity in 2005	Average relative humdity in April 2010	Total precipitation (mm) in April 2010	Maximum temperature in April 2010	Minimum temperature in April 2010
Average relative humidity in 2006	Average relative humdity in May 2010	Total precipitation (mm) in May 2010	Maximum temperature in May 2010	Minimum temperature in May 2010
Average relative humidity in 2007	Average relative humdity in June 2010	Total precipitation (mm) in June 2010	Maximum temperature in June 2010	Minimum temperature in June 2010
Average relative humidity in 2008	Average relative humdity in July 2010	Total precipitation (mm) in July 2010	Maximum temperature in July 2010	Minimum temperature in July 2010
Average relative humidity in 2009	Average relative humdity in August 2010	Total precipitation (mm) in August 2010	Maximum temperature in August 2010	Minimum temperature in August 2010
Average relative humidity in 2010	Average relative humdity in September 2010	Total precipitation (mm) in September 2010	Maximum temperature in September 2010	Minimum temperature in September 2010
Total precipitation (mm) in 2000	Average relative humdity in October 2010	Total precipitation (mm) in October 2010	Maximum temperature in October 2010	Minimum temperature in October 2010
Total precipitation (mm) in 2001	Average relative humdity in November 2010	Total precipitation (mm) in November 2010	Maximum temperature in November 2010	Minimum temperature in November 2010
Total precipitation (mm) in 2002	Average relative humdity in December 2010	Total precipitation (mm) in December 2010	Maximum temperature in December 2010	Minimum temperature in December 2010
Total precipitation (mm) in 2003	Maximum temperature in 2000	Minumum temperature in 2000		
Total precipitation (mm) in 2004	Maximum temperature in 2001	Minumum temperature in 2001		
Total precipitation (mm) in 2005	Maximum temperature in 2002	Minumum temperature in 2002		
Total precipitation (mm) in 2006	Maximum temperature in 2003	Minumum temperature in 2003		
Total precipitation (mm) in 2007	Maximum temperature in 2004	Minumum temperature in 2004		
Total precipitation (mm) in 2008	Maximum temperature in 2005	Minumum temperature in 2005		
Total precipitation (mm) in 2009	Maximum temperature in 2006	Minumum temperature in 2006		
Total precipitation (mm) in 2010	Maximum temperature in 2007	Minumum temperature in 2007		
	Maximum temperature in 2008	Minumum temperature in 2008		
	Maximum temperature in 2009	Minumum temperature in 2009		
	Maximum temperature in 2010	Minumum temperature in 2010		
		Total: 270		

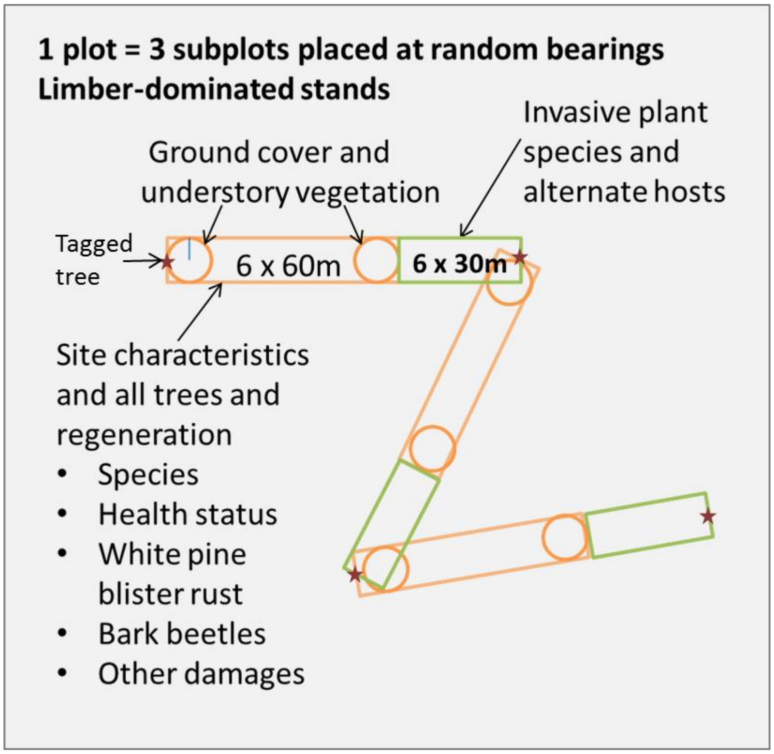


Figure 1.9: Plot diagram from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

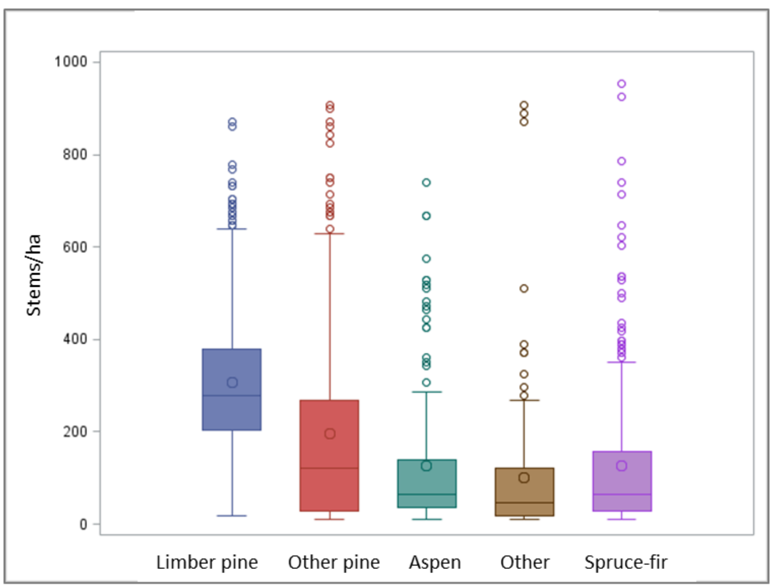


Figure 1.10: Density (stems/ha) of tree species (N = 38,595) from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

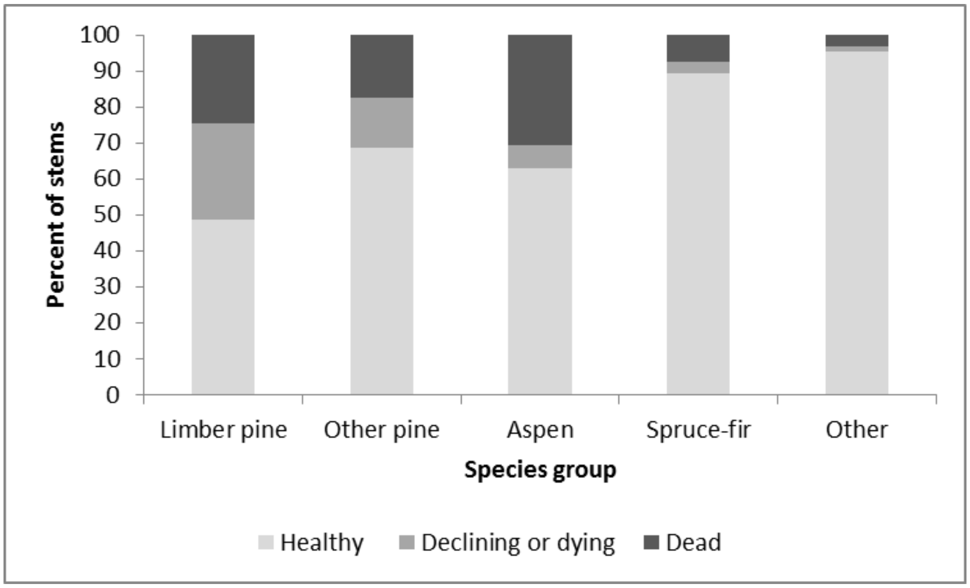


Figure 1.11: Health status of each species group (N = 508) from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012. Healthy includes stems with no visual damage to crown or stem up to 5% damage. Declining includes stems with 6-50% of crown showing symptoms that indicates it is dead or will be and dying includes stems with >50% of crown showing symptoms or is damaged. Dead includes all standing dead stems.

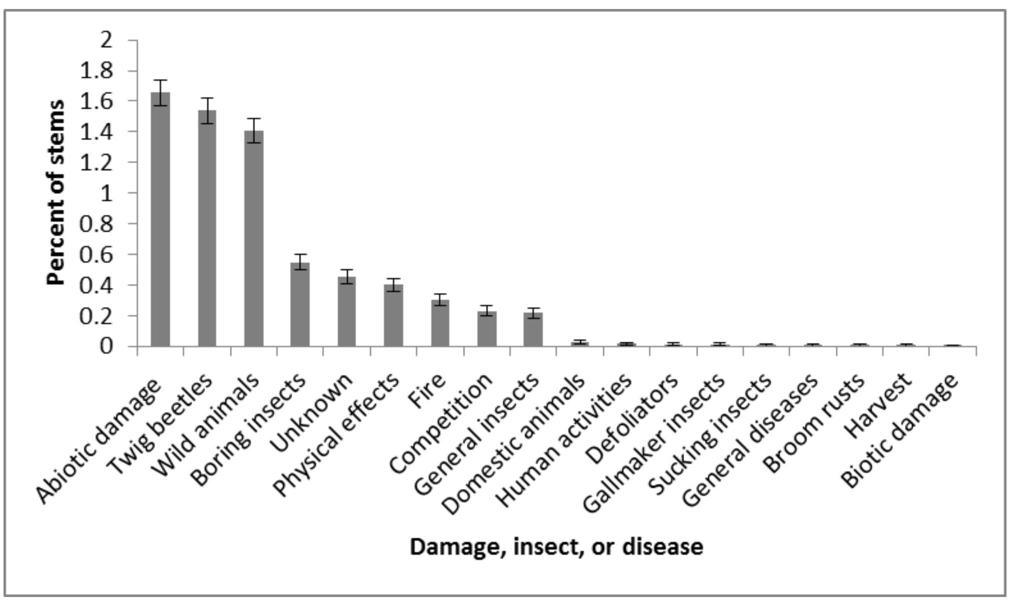
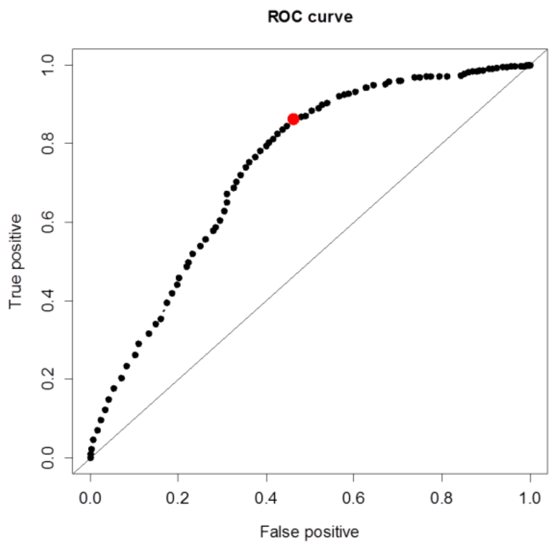
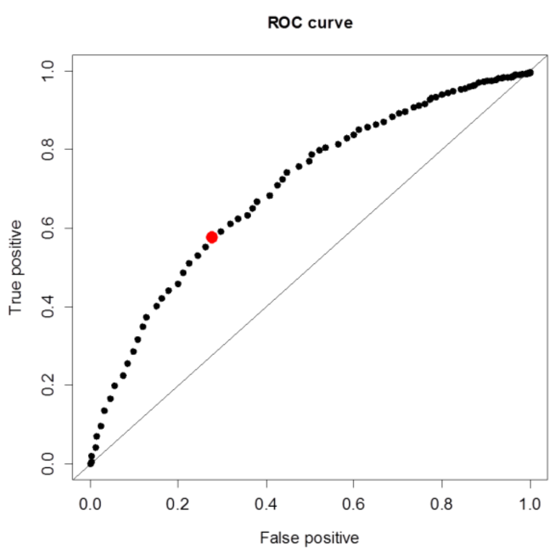


Figure 1.12: Other insects or damages (abiotic and biotic) on live and dead limber pine (N = 508) in Colorado, Wyoming, and Montana in 2011 and 2012.

(a)


ROC curve
True positive
False positive
0.0
0.2
0.4
0.6
0.8
1.0

(b)


ROC curve
True positive
False positive
0.0
0.2
0.4
0.6
0.8
1.0

(c)

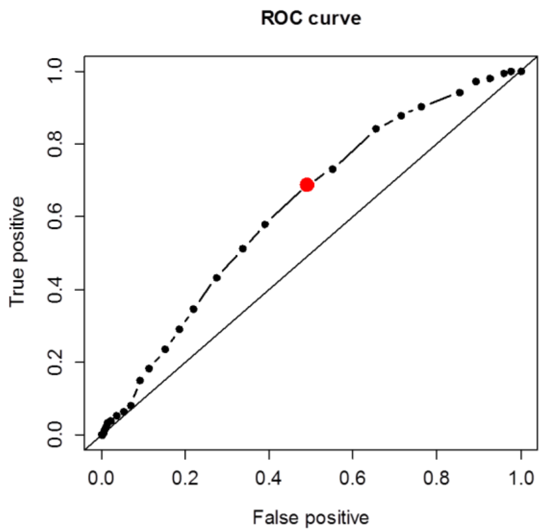


Figure 1.13: Receiver operating characteristic (ROC) curve produced to analyze the logistic regression models predicting occurrence (y/n) of (a) WPBR, (b) bark beetles, and (c) dwarf mistletoe on limber pine on a subplot from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

CHAPTER 2: Manuscript: Limber pine regeneration in forests impacted by white pine blister rust and mountain pine beetle in the central and southern Rocky Mountains

1. Introduction

White pine blister rust (WPBR), caused by the introduced fungal pathogen, *Cronartium ribicola* J. C. Fisch. Major, and more recently, mountain pine beetle (*Dendroctonus ponderosae* Hopk.) are impacting regeneration in limber pine (*Pinus flexilis* James) populations in the Rocky Mountains (Kearns and Jacobi 2007, USDA Forest Service, Rocky Mountain Region 2010). Mountain pine beetle does not directly affect regeneration since the native bark beetle prefers larger diameter trees (Safranyik and Carroll 2006), but mortality of seed-producing trees may limit the opportunity for reproduction.

White pine blister rust may also prevent regeneration by killing cone bearing branches on mature trees (Maloney et al. 2012) and infecting and rapidly killing seedlings which may occur within three years after initial infection (Hoff and Hagle 1990). Heavily infected stands with WPBR are at risk of not regenerating (McKinney and Tomback 2007). In Alberta, low limber pine seedling density in stands heavily impacted by WPBR indicates that populations of limber pine are declining (Langor 2007). While a complete loss of limber pine is not expected from WPBR and mountain pine beetle, these disturbance agents threaten species distribution, genetic diversity, and ecosystem function (Schoettle 2004, Tomback and Achuff 2010).

The fungal rust pathogen, *C. ribicola*, has a complex life cycle with two hosts required and five spore stages. The fungus is capable of infecting five-needle white pines in the subgenus *Strobus* and using species of *Ribes*, *Castilleja*, and *Pedicularis* as alternate hosts (McDonald et al. 2006, Mulvey and Hansen 2011). Infection occurs through the needles of susceptible white pines during late summer and fall under conditions of high relative humidity and the fungus then continues to grow into the branch, ultimately resulting in cankers which may girdle the branch or main stem. Aeciospores produced on the pine tree are fairly durable and can occasionally be windblown several hundred kilometers via atmospheric transport to infect alternate hosts leaves (Frank et al. 2008). Infective, less durable basidiospores produced in late summer to fall on the leaves of the alternate hosts are windblown up to 27 kilometers to the susceptible pines (Zambino 2010).

Limber pine occupies a patchy but extensive, native latitudinal range, reaching from southern California to Alberta, Canada and a broad elevational distribution, from 900 m in North Dakota to 3800 m in Colorado (Gundell 1974, Steele 1990). Stress-tolerant limber pines can be found from lower to upper treeline, but frequent rocky, windswept areas and prevail on xeric sites where competition from other species is minimal (Schoettle and Rochelle 2000). In the central and southern Rocky Mountains, shade-intolerant limber pine occurs in pure stands or may occur in association with lodgepole pine (*Pinus contorta* Douglas ex Loudon), Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), quaking aspen (*Populus tremuloides* Michx.), Rocky Mountain juniper (Juniperus scopulorum Sarg.), and occasionally whitebark pine (*Pinus albicaulis* Engelm.) (Peet 1981, Steele 1990).

Limber pine is valued for its ecological, aesthetic, and cultural importance. They are long-lived, stress-tolerant trees that aid in erosion and avalanche reduction, and often grow in sites that other species cannot (Schoettle 2004). Limber pine is frequently the first species to colonize a burn area, via long-distance dispersal by birds in the family Corvidae which include

Clark's nutcrackers (*Nucifraga columbiana* Wilson) and pinyon jays (*Gymnorhinus cyanocephalus* Wied) and may aid in the establishment of understory species (Baumeister and Callaway 2006) or spruce and fir at high elevations by providing shelter (Rebertus et al. 1991, Donnegan and Rebertus 1999). Limber pines provide wildlife habitat and the seeds are a food source for corvids, pine squirrels (Hutchins and Lanner 1982), and bears (McCutchen 1996).

Availability of limber pine seed may be affected by dispersal mechanisms, seed predation, and damage agents. Like other stone pines of the subgenus Strobus, limber pine seeds are wingless, but lack indehiscent cones like other stone pines, thus limber pine cones scales will open readily when dry and seeds or whole cones may fall to the ground providing a source of regeneration in existing stands. Long distance seed dispersal by Clark's nutcrackers (Lanner and Vander Wall 1980) facilitates regeneration by permitting germination of a small percentage of viable seeds that remain in the bird's caches (Tomback 1982, Lorenz et al. 2011). Regeneration may be inhibited by seed predation by pine squirrels (Benkman, Balda, and Smith 1984, Benkman 1995, Siepielski and Benkman 2007) and by cone and seed insects (Potter and Green 1964, Benkman, Balda, and Smith 1984, Schoettle and Negron 2001).

Several factors may influence limber pine regeneration during seedling establishment, including site factors, soil, ground cover type, microsite or "nurse" objects, competition, growth rate, overstory composition, damage agents, and meteorological conditions. Regenerating stands may occur on xeric sites, favor a windswept, shelter-less environment, are resistant to major abiotic disturbance events (Shankman and Daly 1988, Rebertus et al. 1991). Understory vegetation may act as competition and limit limber pine regeneration (Looney and Waring 2012) or may facilitate establishment by providing protection for the seedling (Maher et al. 2005). Microsite or "nurse" objects such as logs or rocks may also offer physical protection to developing seedlings (Tomback, Sund, and Hoffmann 1993, Coop and Schoettle 2009). Due to a low density and bare soil surface, open-canopy stands of limber pine offer suitable habitat for recruitment (Webster and Johnson 2000). Mortality of overstory trees due to bark beetles can create gaps in the canopy (Raffa et al. 2008) which may promote regeneration (Larson and Kipfmueller 2010). Seedling survivorship at high elevations may benefit from closed canopy stands by protecting existing seedlings from daytime solar radiation and night time heat loss (Casper 2013, Germino and Smith 1999). The slow growth rate of seedlings, typically when suppressed (Veblen 1986), allows for longer vulnerability to biotic and abiotic disturbance agents, including WPBR, temperature extremes, and drought, and it may take many years until reproductive maturity is reached (McCaughey and Schmidt 1990).

Knowledge of the density and health of limber pine seedlings is a major factor in managing for the continued existence of limber pine in pure and mixed conifer stands in the central and southern Rocky Mountains. Only one study (Smith et al. 2013) has addressed the status of limber pine seedlings in established stands, and the study area was in the Northern Rocky Mountains of Alberta and British Columbia. However, no studies have addressed the status of limber pine seedlings, density, impact of white pine blister rust, or factors that influence limber pine regeneration in the central and southern Rocky Mountains. Thus, the objectives of this study were to (*i*) assess site, stand, and health characteristics of limber pine seedlings in areas impacted by white pine blister rust and mountain pine beetle in northern Colorado, Wyoming, and Montana and (*ii*) determine factors that impact limber pine seedlings, including site, stand, groundcover, and meteorological characteristics. An additional objective was to establish an extensive set of plots that could be used to monitor the status of limber pine seedlings over time.

2. Materials and Methods

Site, stand, and health characteristics of limber pines were assessed by determining the size and status of all living and standing dead mature trees and seedlings in fixed area plots within limber pine dominated stands. Recorded data included the occurrence and severity of white pine blister rust (WPBR), bark beetles, and other damages on the trees. Site features (elevation, aspect, slope percent, slope position, stand structure, and disturbance history) were noted within plots along with the amount and type of groundcover, invasive plant species, and occurrence of alternate hosts of WPBR. Plots were established in stands previously sampled and stands not previously sampled. Previously sampled stands were included in the study to address change since the most recent mountain pine beetle outbreak. Limber pine seedling density and proportion of seedlings with WPBR were modeled to determine the influence of site, stand, and climate characteristics.

2.1. Study areas

The geographic range of our monitoring study in the southern Rocky Mountains included the eastern most mountain range of the Rocky Mountains in northern Colorado (Front Range) and in Wyoming we included the southeastern mountain ranges (Medicine Bow and Laramie) and next mountain range of the Rocky Mountains to the west (Sierra Madre). The central Rocky Mountains included additional mountain ranges of the Rocky Mountains to the west (Wind River Range, Absaroka Range) and the northeastern mountain range (Bighorn Mountains), with all minor mountains and basins in between and one mountain range in southern Montana (Pryor Mountains) and another in eastern Montana (Terry Badlands) (Figure 2.1). We conducted surveys on twenty-five study areas in these geographic areas that were defined by government management unit boundaries and geographic sections of mountain ranges (Table 2.1, Figure 2.1).

2.2. Stand selection

2.2.1. Stands previously sampled

Potential plot locations in each study area were developed from the USDA Forest Service Aerial Detection Survey data on areas with mountain pine beetle-caused mortality in limber pine and GPS location data from previous sampling and monitoring efforts by Kearns and Jacobi (2007) and Burns et al. (2011). Using the USDA Forest Service Rocky Mountain Resource Inventory System database to determine the presence of limber pine, Kearns and Jacobi (2007) poststratified to capture varying site conditions and sampled limber pine across an elevational gradient that reflected that of the study area. We used a random stratified sample of these locations so there was relatively equal number of plots with low and high rust infestation and presence or absence of bark beetle outbreak. A range of stands were sampled with varying duration since bark beetle outbreak. Where possible, a minimum of 24 plots per study area were installed to account for low and high WPBR infestation levels and presence or absence of bark beetle-caused mortality with six plots of each. If an insufficient number of stands were found for a particular category, then remaining plots were selected to fill the other stratification variables equally. Plot number within a study area varied depending on the amount of the area with limber pine, previous knowledge of the variation in WPBR incidence and severity, aerial detection data on mountain pine beetle incidence, and accessibility.

2.2.2. Stands not previously sampled

Potential plot locations were selected in each study area where no prior surveys were conducted for WPBR. The areas were based on known records of host location, aerial detection information on MPB-caused mortality, and local knowledge of host location. A stratified random sample of these locations was conducted so there were relatively equal numbers of plots below and above the mid elevation of the limber pine distribution in the study area and presence or absence of bark beetle-caused mortality. Where possible, a minimum of 24 plots per study area were installed to account for two elevation ranges and bark beetle infestation and six plots of each. Remaining protocol followed that of the stands previously sampled.

2.3. Survey methods

2.3.1. Plot establishment

To ensure a reasonable sample of limber pine in our monitoring study, plots were placed in stands with at least 40% adult limber pine (stems/ha). Plots were randomly located at least 10 m from a road within limber pine stands. A plot consisted of three 60 x 6 m fixed area subplots (0.108 ha) that were used for tree assessments with an invasive species/alternate host plot (30 x 6 m) placed after each 60 x 6 m subplot (0.054 ha) and were placed contiguously at random bearings within the stand. Two circular fixed area subplots with a 3 m radius were placed 3 m from each end within the 60 x 6 m subplots to record ground cover and understory vegetation. The series of three 60 x 6 m subplots containing the two 3 m radius circular fixed area plots and 30 x 6 m interval plots in an area defined the plot. The beginning of each subplot and the end of the third subplot were identified by tagging one tree at the center of the plot width and by GPS so the plots can be monitored in the future. Using these methods, 508 plots were established in 2011-2012.

Within each 60 x 6 m subplot, the following data were recorded: elevation (m), aspect (degrees), slope percent, slope position (backslope, footslope [included toeslope and valley bottom], shoulder, summit), stand structure (closed canopy multistory, closed canopy multistory with open individuals and/or open scattered clumps, closed canopy single story with open individuals and/or open scattered clumps [includes mosaic of closed canopy single and multistory], open canopy scattered individuals and/or open canopy scattered clumps), and disturbance history (fire, grazing, other human disturbance, tree cutting).

2.3.2. Trees

Trees were defined as being >1.37 m in height, with no minimum diameter. Within each subplot, the following data were recorded for all tree species, standing dead and alive with a dbh (diameter at breast height) at 1.37 m in height: species, crown class (dominant/co-dominant, intermediate, open, overtopped/understory), dbh to nearest cm using a Biltmore stick, dead or live, percent crown dieback (percentage of dead foliage as compared to the entire crown), dwarf mistletoe rating (DMR) (Hawksworth 1977), bark beetle presence (none or successful bark beetle bole attack). Within each subplot, total number of WPBR cankers was recorded for all limber pine, standing dead and alive with a dbh at 1.37 m (no minimum diameter). Cankers were identified as such if two of the following were present: abnormal swollen branch, blistered branch or stem, aecia present, roughened resin stained bark, or expanding areas of squirrel bark removal. Binoculars were used to identify cankers in taller trees. Trees growing in clumps were considered individual stems if they forked below 1.37 m height and were growing at an angle greater than 45° above horizontal.

2.3.3. Seedlings

Seedlings were defined as being <1.37 m tall, regardless of age. Within each subplot, the following data were recorded for all seedlings, counts of standing dead and alive stems <1.37 m tall (stems in clusters were counted as individuals): species, 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 [0-5 years] = no green needles but some red needles and fine twigs present, old dead [5-10 years] = no fine twigs or needles present, >50% bark still present), and height to the nearest cm. Within each subplot, the following data were recorded for all limber pine seedlings: presence of WPBR, up to two microsite objects that were at least 10 x 10 cm and within 1 m of limber pine seedling (tree, stump, log, rock, shrub), up to two most prevalent ground cover types within 1 m of limber pine seedling (soil, litter, rock, tree/log, lichen/moss, graminoids, shrubs, forbs), type of up to two damages affecting 5% or more of the seedling, and terminal growth, in millimeters, of terminal leader for the previous two years.

2.3.4. Ground cover

Within each circular 3 m subplot, the following data were recorded: percent of area occupied by ground cover type and up to three of the most prevalent shrub species with percent of area occupied by each of those species. To test our analysis of microsite object and groundcover around limber pine seedlings, we used the center point of each circular fixed area subplot as a control point and recorded up to two microsite objects and within 1 m of the center point and up to two most prevalent ground cover types within 1 m of the center point.

2.3.5. Interval plots (invasive species and WPBR alternate hosts)

In the invasive species/alternate host plot (30 x 6 m), the presence and size in m^2 of the ground area occupied by any invasive weed species from the USDA Natural Resources Conservation Service Introduced, Invasive, and Noxious Plants for Colorado, Wyoming, and Montana (plants.usda.gov) and WPBR alternate hosts (*Ribes*, *Castilleja*, and *Pedicularis*) were recorded. Presence and ground area occupied by *Ribes* species were only recorded in previously non-monitored plots.

2.4. Meteorological data

Meteorological data were obtained from the PRISM dataset (Daly et al. 2002) provided by FHTET (USDA FS Forest Health Technology Enterprise Team, Fort Collins, CO). For each plot, meteorological data included 30-year (1981-2010) monthly averages on a 1-km resolution grid for daily minimum and maximum temperatures (°C), precipitation (mm), relative humidity (%), and additional meteorological variables such as drought frequency, growing degree days, and seasonal moisture index, totaling 133 variables (Appendix II, Table 2.14). We also screened each daily temperature minimum, maximum, precipitation, and relative humidity averaged for the individual months from May to September and for the two periods of May–June and July–September.

Additional monthly and yearly meteorological data was extracted from Daymet Daily Surface Gridded Data (Thornton et al. 2012). Daymet only provides daily water vapor pressure ambient values (VP_{amb}), so relative humidity calculations were produce using calculations from Zimmermann and Roberts (2001). For each plot, extracted meteorological data included monthly and yearly averages on a 1-km resolution grid from 2000-2012 for minimum and maximum temperatures (°C) and relative humidity (%) and monthly and yearly totals for precipitation (mm), totaling 270 variables (Appendix II, Table15). For meteorological data that would be potentially related to recent WPBR infection on limber pine seedlings, we formulated variables from the extracted Daymet data for average minimum and maximum temperature and relative humidity, and average total precipitation for the two periods of May–June and July–September for 2005-2011. For meteorological variables that would be potentially related to the last two years of terminal growth (prior to the years sampled, 2011 and 2012) in limber pine seedlings, we formulated average minimum and maximum temperature for May-September, May-June, and

July-September, as well as average total precipitation for May-September, winter (October-April), and total year for each pair of years: 2006-07, 2007-08, 2008-09, and 2009-10.

GIS layers with stream distributions from the USGS National Hydrological High Definition Dataset (available at http://nhd.usgs.gov/) were used to estimate the density of perennial and intermittent streams within a 1-km radius of each survey plot (km/km2). Stream density was used as a surrogate measure for the location of *Ribes* species that occupy moist or riparian sites.

2.5. Data analyses

Data transformations were carried out on certain tree and seedling data prior to any analysis. Stem density was calculated on the total count of live plants in the area of the three subplots established. WPBR incidence was calculated as the number of live infected seedlings/number of live evaluated seedlings. Species other than limber pine and aspen were combined into general groups: other pines included lodgepole, ponderosa, and whitebark pine, spruce-fir included Douglas-fir, subalpine fir, Engelmann spruce, and white spruce [*Picea glauca* (Moench) Voss], and other species included Rocky Mountain (*Juniperus scopulorum* Sarg.) and Utah juniper [*Juniperus osteosperma* (Torr.) Little].

All data analyses were performed using SAS software, Version 9.3 of the SAS System for Windows. Copyright © [2002-2010] SAS Institute Inc., Cary, NC, USA. Simple descriptive statistics were produced for seedling density (stems/ha), basal area, dbh, mean height, health status, other damages, and incidence of WPBR by study area and presented in Table 2.1 and Figures 2.2 and 2.3. Overall means and means by study area were determined using plot-level means. Least square means for occurrence of live limber pine seedlings on a plot in three height classes (s: small 0-45.7 cm, m: medium 45.7-91.4 cm, and t: tall 91.4-137 cm) were produced using PROC GLIMMIX with values adjusted for study area and height class. Error bars are ± half approximate LSD. Due to skewed data, we report both the median and mean value for seedling density (stems/ha). To establish percent cover of *Ribes*, we combined our collected *Ribes* data for plots not previously monitored with data from Kearns and Jacobi (2007) for the previously monitored plots.

To determine the most prevalent ground cover types and microsite objects within a 1 m radius of limber pine seedlings, mean probability of occurrence of groundcover type and microsite objects next to seedlings were compared to that of the control points using a paired t-test (PROC TTEST) with a critical level of significance set as $P < 0.0001$.

Using the subplot-level variables and using only subplots with limber pine seedlings (N=1087), linear regression was used to determine which variables can predict (a) density (stems/ha) of limber pine seedlings, (b) proportion of limber pine seedlings with WPBR, and (c) terminal growth (mm) of limber pine seedlings. Stem density (stems/ha) and basal area (m^2/ha) variables were transformed to a $\log_{10}$ scale and proportion of seedlings infected with WPBR and percent cover of *Ribes* were square root transformed to normalize skewed data. Tested variables included those in each category: plot, trees (stems > 1.37 m tall), seedlings (stems ≤ 1.37 m tall), ground cover, WPBR alternate host, and meteorological data. For (a), (b), and (c), we screened each category of variables using PROC GLMSELECT with selection=lasso (least absolute shrinkage and selection operator) (stop=sbc choose=sbc [specifies Schwarz criterion as a stopping criterion]) with nsamples=1000 (modifies number of samples used to 1000). Selected variables had to be in at least 20% of those 1000 models. Next, selected variables were incorporated into a model using PROC MIXED with ddfm=kr (requests that degrees of freedom method is Kenward-Roger) for (a), (b), and (c) with study area as a random effect. Using backward elimination, we manually decided which variable to remove, ultimately using p=0.001 for significance, and watched for large changes in regression coefficients, making sure that there wasn't a problem with multicollinearity. For (a), (b), and (c), Pearson correlations (using PROC CORR), with critical level of significance set as $P < 0.0001$, and scatter plots were examined to review the response distribution to ensure lack of high leverage. Final models were fit using PROC MIXED with ddfm=kr with study area as a random effect. For (a) and (b), relationship between fixed effect variables and response variable were plotted using mean values for the other fixed variables and the 5th, 25th, 50th, 75th, and 95th percentiles of the variable being plotted (Figures 2.5 and 2.6). Predicted values were back transformed.

3. Results

3.1. Seedling presence, density, and health status

Throughout the study, 508 plots (82.3 ha) were established in twenty-five study areas. Surveyed plots ranged in elevation from 826 to 3,140 m and averaged 2,376 m (Table 2.1). We examined 24,597 seedlings ≤ 1.37 m in height; of those, 8,013 or 33% were limber pines, 14% were other pines and juniper which include lodgepole pine, ponderosa pine, whitebark pine, Rocky Mountain juniper, and Utah juniper, 34% were aspen, 19% were spruce-fir which included Douglas-fir, subalpine fir, Engelmann spruce, and white spruce. Mean height of limber pine regeneration was 72.5 cm, while mean height of other pines was 72.9 cm and both aspen and spruce-fir were 66.8 cm.

Overall, live seedlings were present in 97% of plots and 84% of subplots, while live limber pine seedlings were found in 91% of plots and 71% of subplots. Live limber pine seedling presence was lowest and found in only 29% and 42% of subplots in the northern and southern Absaroka Range. When dividing live limber pine seedlings into three height classes: small 0-45.7 cm, medium 45.7-91.4 cm, and tall 91.4-137 cm, overall, live limber pine seedlings in the small height class were present in (Means ± ½ LSD) 68 ± 2.6% of plots, while live limber pine seedlings in the medium and tall height classes were present in 78 ± 2.6% and 79 ± 2.6% of plots (Appendix II, Figure 2.7a and b). Six study areas (Ferris Mountains, Absaroka south and north, Bighorn Mountains south and north, and the Pryor Mountains) fell below this average in all three height classes (Appendix II, Figure 2.7a and b).

Live limber pine seedling density (n = 508 plots) ranged from 0 to 1,935 stems/ha with a mean (± standard deviation, median) of 141 (± 201, 74) stems/ha (Table 2.1). Live seedling density of other pines was 64 (± 274, 0) stems/ha, aspen 136 (± 370, 0) stems/ha, and spruce-fir 83 (± 300, 0) stems/ha (Table 2.1). Mean live limber pine seedling density, including plots with no live limber pine seedlings, for small, medium, and tall seedlings was 55 (± 117, 19), 52 (± 78, 28) stems/ha, and 34 (± 44, 19) stems/ha, respectively (Table 2.2). Over half (13) of all of the study areas fell below this average in all three height classes (Table 2.2). Live limber pine seedlings were divided into density classes (zero: no seedlings, low: >0 – 55 stems/ha, medium: >55 – 140 stems/ha, and high: >140 stems/ha). Overall, 9% of plots lacked any live limber pine seedlings and 29%, 32%, and 30% of plots have low, medium, and high densities, respectively (Figure 2.2). Study areas with greater than 1/3 of plots in each the medium and high density classes include those in the Laramie Mountains, Sweetwater Basin, and Montana (Figure 2.2). Those with greater than 9% plots with no seedlings and/or 1/3 of plots in the low density category include those in the Wind River Range, Absaroka Range, Bighorn Basin and Mountains (Figure 2.2).

Most (85%) limber pine seedlings were considered healthy, while 11% were declining or dying, and 4% were dead (Appendix II, Table 2.7). Only mortality of aspen was higher at 10%, while mortality of other pines and spruce-fir was 1%. Absaroka north contained highest percent of limber pine seedling mortality at 13%, followed by Bighorn east at 11% and the Green Mountains at 10%. White pine blister rust was the primary damage agent on live and dead limber pine seedlings and occurred in 20 of the 25 study areas and on 30% of the 508 surveyed plots. Overall, 5.3% of live and 1.6% of dead limber pine seedlings were infected with WPBR. Mean incidence of live and dead seedlings ranged from 0% in Laramie Peak west, the Medicine Bow Mountains, and the Terry Badlands, to 33% in Absaroka south. Incidence of WPBR on live limber pine in the small, medium, and tall height classes increased with height and was 0.8%, 5.4%, and 9.2%, respectively (Figures 2.3a and b).

Other diseases and damages on the evaluated limber pine seedlings were infrequent but did occur in all study areas and on 49% of the 465 plots with limber pine seedlings. Those that did infect or damage 5% or more of the seedling included physical damage (includes broken or dead top) which occurred in 24 study areas, on 178 plots, and on 4.5% of all evaluated limber pine seedlings, dwarf mistletoe occurred in 16 study areas, on 35 plots, and on 2.8% of seedlings; abiotic damage occurred in 10 study areas, on 24 plots, and on 0.4% of seedlings; and insects occurred in 6 study areas, on 23 plots and on 0.6% of seedlings (Appendix II, Figure 2.10).

3.2. Ground cover and microsite object

Across all study areas, grass, with a mean of 23.7%, occupied the greatest area within the ground cover plots, followed by shrubs at 18.8%, and litter at 13.4%. Thirty-two different shrub species were noted on the plots and the most common shrub species was big sagebrush (*Artemisia tridentata* Nutt.) (9.2%), followed by common juniper (*Juniperus communis* L.) (4.1%), and bitterbrush (*Purshia tridentata* (Pursh) DC.) (1.3%). Other common shrub species included snowberry (*Gaultheria* L.) (0.8%), fringed sagebrush (*Artemisia frigida* Willd.) (0.7%), kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.) (0.6%), and wax current (*Ribes cereum* Douglas) (0.53%).

When compared to control points (P<0.0001), limber pine seedlings were 19% more likely to occur with litter and 18% more likely to occur with rock, and 4% less likely to occur with forbs, 14% less likely with grass, and 6% less likely with bare soil (Figure 2.4a). There was no significant difference in ground cover type between seedlings and control points for lichens, shrubs, or trees (Figure 2.4a). Seventy-two percent of limber pine seedlings were next to objects while 63% of control points were next to objects. When compared to control points (P<0.0001) , seedlings were 6% more likely to be next to a rock and 11% more likely to be next to a tree and 11% less likely not occur next to a microsite object (Figure 2.4b). There was no significant difference in microsite object type between seedlings and control points for logs, shrubs, or stumps (Figure 2.4b).

3.3. Invasive plant species

Invasive plant species were observed on 19% of plots in 68% of study areas. The study areas with the greatest number of plots with invasive plant species included the Bighorn Mountains (eastern, southern, and northern) with 28 plots followed by Muddy Mountain with 10 plots. Over all the study areas, 10 different invasive species were noted: Canada thistle (*Cirsium arvense* [L.] Scop.), cheatgrass (*Bromus tectorum* L.), musk thistle (*Carduus nutans* L.), salsify (*Tragopogon porrifolius* L.), Scotch thistle (*Onopordum acanthium* L.), bull thistle (*Cirsium vulgare* [Savi] Ten.), yellow toadflax (*Linaria vulgaris* Mill.), common mullein (*Verbascum thapsus* L.), myrtle spurge (*Euphorbia myrsinites* L.), and golden rod (*Solidago* L.). Bull thistle, listed as a noxious weed in Colorado but measured in all three states for consistency, was the most commonly observed invasive species and was found on 32 plots, followed by musk thistle on 20 plots, Canada thistle on 11 plots, and cheatgrass on 9 plots. Across all study areas, ground area occupied by invasive species was an average of 261.6 m^2. Cheatgrass occupied the greatest area with a mean of 2,212.0 m^2, followed by yellow toadflax (416.7 m^2), and common mullein, Canada thistle, musk thistle, Scotch thistle, and bull thistle (decreasing from 50.0 - 23.8 m^2, respectively).

3.4. Alternate hosts of white pine blister rust

White pine blister rust alternate hosts were observed in all evaluated study areas. When including data from Kearns and Jacobi 2007, *Ribes* species were found in all 25 study areas, on 47% of plots (338 plots, n=723) and ranged from 5% of plots in the Terry Badlands to 100% of plots on the Ferris Mountains. On plots in which *Ribes* species were measured in this survey, *Ribes* species occupied an average area of 337.9 m^2. *Castelleja* species were found in 97 plots in 21 study areas and occupied an average area of 35.8 m^2. *Pedicularis* species were the least abundant alternate host and were found in only 1 plot and occupied an average area of 0.3 m^2.

3.5. Seedling models

3.5.1. Limber pine seedling density

We used linear regression analysis to determine the variables that predict density (stems/ha) of limber pine seedlings on a subplot. Variables in all categories: plot (site features), trees, seedlings, ground cover, and meteorological, were selected in at least 20 percent of the 1000 models after screening each category. Variables selected in the final model include $\log_{10}$ stems/ha of limber pine trees (mean = 2.48, std = 0.45, P = 0.30, p-value < 0.0001), $\log_{10}$ stems/ha of all live trees (mean = 2.62, std = 0.36, P = 0.27, p-value < 0.0001), limber pine seedling height (cm) (mean = 72.43, std = 26.89, P = -0.27, p-value < 0.0001) and grass (percent cover) (mean = 23.72, std = 15.51, P = -0.14, p-value < 0.0001) (Table 2.3). Stems/ha of limber pine trees and stems/ha of all live trees had a positive influence on limber pine seedling density (Figures 2.5a and b) while percent area of grass and limber pine seedling height (cm) were negative influences (Figures 2.5c and d). Density (stems/ha) of both other pines and aspen seedlings were selected in at least 20 percent of models during category screening, but no variables that represented competition from other regenerating species were selected in the final model. We did not find relationships with basal area (m^2/ha) of overstory mortality due to mountain pine beetle on limber pine seedling density, and for comparison, we modeled aspen seedling density and found the same result.

3.5.2. Proportion of limber pine seedlings infected with WPBR

Linear regression analysis, predicting the proportion of limber pine seedlings infected with WPBR on a subplot, selected two variables in the final model, including a positive influence of both limber pine seedling height (cm) (mean = 73.14, std = 26.71, P = 0.15, p-value < 0.0001) and $\log_{10}$ tree cankers/ha (mean = 1.62, std = 1.27, P = 0.34, p-value < 0.0001) (Table 2.3, Figures 2.6a and b). Since cankers/ha are not data easily accessible to land managers, we ran the same linear regression model without canker variables. Variables selected in the final model included the positive influence of three variables; limber pine seedling height (cm) (mean = 73.14, std = 26.71, P = 0.15, p-value < 0.0001), crown dieback (percent) of all standing live and dead trees (mean = 28.95, std = 27.59, P = 0.08, p-value = 0.0107), $\log_{10}$ stems/ha of limber pine trees with WPBR (mean = 1.29, std = 0.99, P = 0.31252, p-value < 0.0001) (Table 2.3).

3.5.3. Terminal Growth

We measured the average terminal growth (mm) of the previous two years (from year of measurement) of limber pine seedling growth to determine growth rates and to see if recent bark beetle-caused mortality released seedling terminal growth. The small, medium, and tall seedling classes had average yearly terminal growth (means ± ½ LSD, n = 508), of 23 ± 1.6 mm, 39 ± 1.5 mm, and 58 ± 1.5 mm, respectively. These rates did vary significantly between study areas (Appendix II, Figure 2.13). We did not find any relationship with basal area of recent beetle mortality and terminal growth. However, linear regression analysis found positive relationships with sagebrush (mean = 9.15, std = 11.79, P = 0.30, p-value < 0.0001) and grass cover (mean = 0.39, std = 0.39, P = 0.32, p-value < 0.0001)), seedling height (mean = 72.43, std = 26.89, P = 0.58, p-value < 0.0001) and negative relationship with $\log_{10}$ basal area (m2/ha) of all live trees (mean = 0.87, std = 0.38, P = -0.23, p-value < 0.0001) (Appendix II, Table 2.11, Figure 2.12).

4. Discussion

Limber pine stands heavily impacted by mountain pine beetle and WPBR are at risk of not regenerating. To determine whether limber pine will persist on the landscape based on a snapshot of limber pine regeneration, three main factors were taken into consideration: 1) seedling occurrence 2) seedling density and 3) seedling health, along with additional factors, such as microsite object and competition. Determining factors that influence limber pine regeneration is valuable for future management decisions regarding limber pine.

4.1. Seedling presence

Overall, limber pine seedlings (live and dead) were present on 92% of plots, with eight study areas falling below the mean and four of those were between 54% and 75%. Most of the study areas that fell below the mean were located in the more northern areas of our study, where WPBR has been longer. Smith et al. (2013) found at least one live limber pine seedling in 76% of plots in 2003-2004 and 85% of plots in 2009, indicating that recruitment is continuing to occur; however, there was a reduction in seedlings in the taller height class, suggesting a reduction in survivorship. In another study, southwestern white pine (*Pinus strobiformis*

Engelm.) seedlings were not common but the authors suggested that existence might be explained by a high survivorship rate (Looney and Waring 2012).

4.2. Seedling density

Overall mean live limber pine seedling density, 141 stems/ha, is comparable to the results of a limber pine study in the Rocky Mountains of Alberta and British Columbia where mean density of live limber pine seedlings were 100 seedling sites/ha in 2003-2004 and increased to 150 seedling sites/ha in 2009 (Smith et al. 2013). However, a slight variation in density exists between the studies considering Smith et al. (2013) counted seedling clumps as one unit (seedling sites) and we differentiated individual stems, even if clumped. Our seedling density is low in comparison with a study of limber pine regeneration in sites post-fire on the Front Range of Colorado, where they found two sites at about 290 stems/ha and one at 508 stems/ha (Shankman and Daly 1988). Since no baseline estimate exists to determine the normal or optimal density of limber pine seedlings needed to sustain a stand, it is difficult to determine whether these densities are normal, given the conditions. Limber pine is naturally slow-growing and it may be many years before a stem may reach reproductive maturity. The densities in this study appear low when compared to the density of WPBR impacted whitebark pine seedlings in northern Montana and the Canadian Rockies at 400 stems/ha (Smith et al. 2008). In Alberta, where limber pine is listed as an Endangered species under The Wildlife Act (Government of Alberta 2012), limber pine seedling density may also be especially low in montane areas due to cattle grazing (Langor 2007).

Seedlings occurred in 12% more plots in the tall height class versus the small height class; however, live limber pine seedling density decreased with increasing height class, suggesting low survivorship. Density seemed especially low in the more northern study areas (central Rocky Mountains) where stands have been exposed to WPBR infection for a longer period as compared to the more southern study areas (southern Rocky Mountains). In addition, these same mountains have had long term regional droughts that may have had an effect on seedling survival.

4.3. Seedling health

While most limber pine seedlings were considered healthy, the primary damage agent was WPBR. Overall incidence of WPBR on live seedlings (5.3%) was slightly less than results from Smith et al. (2013), where 8% of live limber pine seedlings in 2003-2004 were infected with WPBR, but greater than 4% when remeasured in 2009. While we did assess dead limber seedlings for WPBR, we found few standing dead stems, likely because of rapid girdling in 3 years (Hoff and Hagle 1990) and a short time to when the seedling fell, which we estimated at 3-5 years. Thus, WPBR-caused mortality is likely higher than what we are able to measure. The study area (Absaroka south) with the lowest live limber pine seedling density (38 stems/ha) also exhibited the greatest incidence of WPBR infection on live and dead seedlings at 33%.

Other diseases, insect, and damages, such as dwarf mistletoe, on limber pine seedlings were not common, likely due to having less exposed surface area and exposure time compared with trees and the short period damaged trees remain standing. The most prevalent damages, aside from WPBR were physical damage, which was often associated with a WPBR infection that had girdled the main stem, and dwarf mistletoe. Our results of finding few additional damage agents are consistent with a limber pine planting study by Casper (2012), who also found few damage agents on limber pine seedlings, noting that herbivory affected less than 1% of seedlings. We might have expected abiotic damages to have affected more than our result of less than 1% of limber pine seedlings, since seedlings are more vulnerable to abiotic stressors such as drought, flooding, temperature extremes, snow and ice, and excessive sunlight (Franklin et al. 1987).

4.4. Ground cover and microsite objects

Ground cover type may aid or inhibit regeneration. Limber pine seedlings occurred more often with non-competing ground cover types, litter and rock, as compared to control points. Looney and Waring (2012) noted a positive relationship between southwestern white pine, another five-needle white pine in close association with limber pine, regeneration and litter abundance, but also with log cover. Some ground cover vegetation may act as competition for limber pine seedlings. Grass occupied the greatest area of our ground cover plots and limber pine seedlings tended to occur less often with grass, results consistent with Jones (1967), who noted a lack of seedlings where grass was prevalent. In addition to grass, seedlings occurred less often with forbs and bare soil, results consistent with a study of southwestern white pine regeneration in which Looney and Waring (2012) found a negative relationship between seedlings and grass, forbs, and bare ground. Coop and Schoettle (2009) found no positive association between ground cover vegetation at the seedling scale. While we found no significant association with shrubs, O'Brien et al. (2007) found a negative impact of shrubs on natural regeneration of Monterey pine (*Pinus radiata* D. Don). We did not look at ground cover with respect to high elevation, but in the subalpine environment, ground cover vegetation may protect seedlings from harsh conditions (Maher et al. 2005). To date, invasive plants are not impacting limber pine regeneration but some of the most at- risk- mountain ranges for limber pine regeneration failure also have the greatest invasive plant populations.

Clark's nutcracker tends to cache seeds near cover and will often do so within 4 m of a tree which is often surrounded by litter (Lorenz et al. 2011). Microsite objects have shown to provide some protection for developing seedlings and may be particularly important in harsh sites and upper treeline (Maher and Germino 2006). Coop and Schoettle (2009) found a strong association between microsite objects and seedlings in sites post-fire, but object type did not matter. Our results were similar in that limber pine seedlings were located more often next to microsite objects such as rocks or trees versus the control points.

4.5. Seedling models

4.5.1. Limber pine seedling density

We were able to determine variables that predict density (stems/ha) of limber pine seedlings using linear regression analysis. Our results indicated that stems/ha of limber pine trees, stems/ha of all live trees, percent area of grass, and limber pine seedling height (cm) were all important variables in predicting limber pine seedling density. We would naturally expect a positive relationship between limber pine seedling density and limber pine tree density since mature, cone-bearing trees provide the seed source for regeneration, and the results of the final model reflected that. A positive relationship between limber pine seedling density and density of all live trees might be explained by the increased amount of cover that an increased density of trees might provide for seedlings. Natural regeneration of Monterey pine benefits from overstory cover (O'Brien et al. 2007) and whitebark pine regeneration is positively associated with total stand density, as well as whitebark pine density (Larson and Kipfmueller 2010). While tree cover reduces sunlight availability, it can provide more stable night time microsite conditions by allowing for warmer and more stable temperatures, exposing seedlings to a less stressful environment (Germino and Smith 2000, Maher et al. 2005). In contrast, Larson and Kipfmueller (2010) found a positive association with MPB-caused overstory mortality and whitebark pine regeneration abundance, indicating a benefit from a gap in the canopy. We found no impact of overstory mortality due to mountain pine beetle on either limber pine or aspen seedlings, which is likely due to the shorter time length between mountain pine beetle infestation (0-5 years) and regeneration establishment and growth. We would expect regeneration release in some impacted areas, given more time since overstory mortality.

A negative relationship exists between grass and limber pine seedling density, which is consistent with Jones (1967), Looney and Waring (2012), and our comparison of limber pine seedlings and control points, with grass being less prevalent near seedlings. This further emphasizes that grass acts as competition and may inhibit limber pine regeneration. The negative relationship between limber pine seedling density and limber pine seedling height (cm) suggests that seedlings are more likely to reach maturity in lower densities.

While Larson and Kipfmueller (2010) found a strong negative relationship between subalpline fir and whitebark pine abundance, as well as relationships with site and meteorological variables, while we found no relationships between limber pine seedling density, competing seedlings of other species, site, or meteorological variables. When looking at the three study areas with the lowest limber pine seedling density: Absaroka south (38 stems/ha) and north (62 stems/ha) and Bighorn south (60 stems/ha), competing species were abundant and greater than 90% healthy in both Absaroka south and Bighorn south. However, in Absaroka north, density of competing species was less than that of limber pine, and both limber pine and spruce-fir regeneration exhibited the highest mortality of all 25 study areas at 13% and 12%, respectively. Those results indicate that in some study areas, competing seedlings are thriving, but in others, lack of competing seedlings may indicate a poor site quality for any regenerating tree species, and this supports our limber pine seedlings density model, suggesting that factors other than competing seedlings are more important in predicting limber pine seedling density.

We expected meteorological variables to impact limber pine seedling density since seedlings are especially vulnerable to extreme meteorological events. However, no meteorological variables were related in our modeling efforts. While longer, warmer growing seasons promote seedling establishment, but also result in higher mortality due to heat-related damages, cooler sites with lower regeneration density result in higher survivorship (Larson and Kipfmueller 2010). Increased growing season precipitation may also increase regeneration (Tomback et al. 1993).

4.5.2. Proportion of limber pine regeneration infected with WPBR

The generalized linear mixed-effects model results indicated that the most important variables that predict the proportion of limber pine seedlings infected with WPBR on a subplot include height and tree cankers/ha. Tomback et al. (1995), Smith et al. (2008), and Smith et al. (2013) each found a positive relationship between seedling height and incidence of WPBR in seedlings which is consistent with the positive relationship we found between seedling height and proportion of limber pine seedlings infected with WPBR. As each suggested, there is likely a higher probability of basidospores landing on a taller seedling due to greater needle surface area or assuming that taller seedlings are older, they have been potentially exposed to WPBR infection for a longer time period. The positive relationship between proportion of limber pine seedlings infected with WPBR and cankers per adult limber pine suggests that trees become increasingly infected, seedlings are also infected. Since basidiospores require conditions of high relative humidity in late summer or fall, we expected the final model to reflect this. While some late fall relative humidity variables (relative humidity in October and November) were selected in at least 20 percent of models during category screening, no meteorological variables were selected in the final model. When eliminating tree cankers/ha, the variables that that predicted the proportion of limber pine seedlings infected with WPBR on a subplot included limber pine seedling height (cm), crown dieback (percent) of all standing dead and live trees, and stems/ha of limber pine trees with WPBR. Relationship with stems/ha of limber pine trees with WPBR suggests that if WPBR is present in the stand on trees, seedlings are also infected. Relationship of crown dieback may suggest that as crown dieback and depletion of overstory occurs, it leaves live seedlings more open and exposed to infection by WPBR.

4.5.3. Terminal Growth

Limber pines occupy areas that do not promote fast growth and seedlings may remain small for many years before release. Our results of average terminal growth measurement indicate that terminal growth rate increases as seedlings age, but on some sites, terminal growth may be very slow or delayed until release. In sites in Colorado and Wyoming, Casper (2012) found limber pine seedlings between 30 and 140 cm tall to range in age from about 12 to 41 years. Median age of limber pine seedlings (≤ 1.4 m tall) (n=8) on a site in the front range of Colorado was 63 years and ranged from 47 to 115 years, supporting the typical slow growth rates of conifers, particularly when suppressed (Veblen 1986). Whitebark pine, also a slow-growing, 5-needle pine, takes a minimum of about 25 years to reach reproductive maturity (McCaughey and Schmidt 1990).

The results of our linear regression analysis predicting terminal growth (mm) of limber pine seedlings indicated that big sagebrush (percent of ground cover), limber pine seedling height (cm), grass (as a dominant ground cover next to limber pine seedlings), and basal area (m2/ha) of all live trees were all important variables in predicting terminal growth of limber pine seedlings. Positive relationships with big sagebrush and grass suggest that these vegetation types indicate a good growing site. We would naturally expect a positive relationship with height since seedlings tend to grow more as they increase in age and height. The negative relationship with basal area of all live trees suggests an impact of canopy or competition from larger trees. While we found no relationships with terminal growth and latitude or meteorological variables, increasing latitude does offer shorter growing seasons and increase in potential for cold-related damages which may reduce terminal growth of seedlings (Bengtson et al. 1967).

4.6. Other factors that potentially impact limber pine regeneration

While we have been able to measure and analyze many factors that potentially impact limber pines and determine if limber pine will persist, several additional factors must be taken into consideration, particularly those affecting limber pine seed. Since seed production of limber pine may be erratic, knowledge of frequency of mast years is valuable in predicting regeneration success. Long-distance dispersal by Clark's nutcracker is key to maintaining some limber pine populations, particularly those impacted by damage agents and with low reproductive capacity. Clark's nutcracker will cache between 35,000 (Tomback 1982) and 98,000 seeds per year (Hutchins and Lanner 1982) and may occur at distances greater than 22 kilometers from the source (Lorenz et al. 2011). Forty-five percent of the cached seeds are not retrieved and germination may occur from remaining viable seeds situated in sites ideal for growth (Tomback 1982). Lorenz et al. (2011) found that only 15% of whitebark pine seeds were cached in sites suitable for germination.

Pine squirrels reported to be the most important seed predator of limber pine, and when present in a limber pine stand, they dominate seed harvest over Clark's nutcracker (Siepielski and Benkman 2007). A study in Arizona by Benkman et al. (1984) found that red squirrels (*Tamiasciurus hudsonicus*) leave less than 20 percent of limber pine cones after harvest of unopened cones in dense stands. In sites without red squirrels, Clark's nutcracker extracted seeds from open cones which consisted of about 70 percent of the cone crop (Benkman et al. 1984). In mixed conifer stands that include whitebark pine, pine squirrels do not rely solely on whitebark seeds, thus, their populations are not affected by a decline in whitebark pine and seed harvest can exacerbate a reduction in seed availability for dispersal and regeneration in stands affected by mountain pine beetle and WPBR (McKinney and Fiedler 2010). In addition to directly reducing propagule availability by consumption, harvest of limber pine seeds by pine squirrels indirectly restricts the evolution of traits (i.e. more seeds per cone) that encourage dispersal of seeds by Clark's nutcracker (Benkman 1995, Siepielski and Benkman 2007). Cone and seed insects are known on limber pine and may also impact seed available for regeneration but the amount of impact is not known and thus, should be an important factor in future genetic work (Benkman et al. 1984, Potter and Green 1964, Schoettle and Negron (2001).

Climate change, one of the more difficult factors to measure impact on regeneration, will likely influence future limber pine distribution, and regional warming has already been identified as the potential cause of increased mortality rates in western U.S. trees (van Mantgem 2009). Future meteorological conditions may render some limber pine habitat unsuitable for regeneration and also may allow for limber pine regeneration in environments that were not previously suitable for regeneration. Lack of precipitation can lead to drought –stress and winter desiccation. While we would expect increasing temperatures and drought to negatively impact regeneration, such conditions would also not be ideal for WPBR infection.

4.7. Management implications

Study areas with low limber pine seedling density and a high incidence of WPBR should be considered areas of high priority for restoration. A study by Maloney et al. (2012) found a negative relationship between whitebark pine cone production and WPBR and suggests that this may result in declining whitebark pine populations. As seed sources are impacted by WPBR and MPB, stands with existing opportunistic seed predator populations limit opportunity for seed dispersal and regeneration (McKinney and Tomback 2007). In whitebark pine stands, it is estimated that Clark's nutcracker requires at least 1000 cones/ha to remain in a stand and disperse seed, and a basal area of 5 m^2/ha is estimated to produce that amount (McKinney et al. 2009). However, Barringer et al. 2012 noted that while Clark's nutcracker is more likely to visit whitebark stands with more cones, they do still visit stands with little cone production. As mortality increases from disturbances like white pine blister rust and the mountain pine beetle, propagule availability decreases and the probability that limber pine seeds may be dispersed by Clark's nutcracker to newly burned areas to regenerate, decreases (Coop and Schoettle 2011). Facilitating and maintaining stands of limber pine is essential to promoting natural selection to encourage the development of resistance mechanisms to WPBR (Loo 2009). Our results indicate that stands should be managed to increase density of limber pine trees, however, increased density could make the stand more susceptible to bark beetle attacks. Managing limber pine stands, particularly those with little WPBR impact, for multiple age classes may allow for increased regeneration (Schoettle and Sniezko 2007) and would provide some insurance against bark beetle attacks. Since seed predators prefer mixed conifer stands as opposed to whitebark-dominated stands, most seed dispersal may originate from whitebark-dominated stands and management of these stands may need not be as intensive (McKinney and Fiedler 2009). Limber pine regeneration may benefit from natural disturbance, such as fire, or creation of openings and microsite objects, but will take many years to see results (Coop and Schoettle 2009). Thinning treatments may not benefit seedlings as much as mature trees (Keane et al. 2007). Our findings indicate that seedling establishment benefits from areas surrounded by litter and rock, away from competition from grass and forbs, and next to microsite objects, particularly rocks and trees. At high elevations, seedlings may benefit from the protection of tree cover to maintain warmer night time temperatures and potential reduction from freezing injury (Germino and Smith 1999). Our results also indicate that limber pine regeneration density benefits from an increase in overstory density.

Proposed restoration efforts include identifying and collecting potentially WPBR resistant genotypes, testing of seed for genetic resistance, and outplanting of WPBR resistant stock (Schoettle and Sniezko 2007). Limber pine has shown to exhibit multiple resistance mechanisms to WPBR, including complete resistance in some families by way of the newly discovered *Cr4* resistance allele, which was found in 0 to 14 percent, and averaging 5 percent, of limber pine in the southern Rocky Mountains (Schoettle et al. 2014). A few studies (Smith et al. 2011, Casper 2012) have made recommendations for outplanting limber pine seedlings with good survival success. Smith et al. (2011) recommended outplanting seedlings, instead of seed, and in clusters for a greater survival rate. Planting near a microsite object, such as a rock or tree, particularly on higher elevations or harsh sites or may also provide protection for developing seedlings (Maher and Germino 2006, Smith et al. 2011). Casper (2012) recommends planting seedlings on the north or west side of microsite objects and under canopy cover.

In most study areas, limber pine regeneration will likely persist, however, much uncertainty exists with future meteorological influence. A few study areas, including Absaroka south and north, and Bighorn north fall well below the overall means in each presence, density, and health, indicating that some local limber pine populations may be declining in these study areas. As WPBR continues to spread and intensify, low-risk stands and previously unaffected stands will be at risk of decline. It would be beneficial to employ management decisions that encourage limber pine regeneration. While we present a snapshot of the current state of limber pine regeneration, future monitoring of our plots would provide the needed measure of regeneration over time, particularly in areas of declining limber pine, and thus determine the trajectory of these stands.

Tables and Figures

Table 2.1: Density (stems/ha) of live seedlings in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

State, geographic range, and study area	plots[a]	mean elevation (m)	limber pine					other pine[b]					aspen					spruce-fir[c]				
			median	min	max	mean	std	median	min	max	mean	std	median	min	max	mean	std	median	min	max	mean	std
Colorado																						
Front Range																						
Boulder County	14	2735	51	0	1019	194	326	65	0	694	129	184	139	0	3806	547	993	19	0	889	133	246
North	25	2669	65	0	509	96	118	56	0	1454	153	293	148	0	1954	307	443	9	0	176	29	46
Wyoming																						
Laramie Mtns																						
Pole Mtn	24	2544	301	28	1657	373	335	106	0	630	157	168	255	0	1352	378	385	0	0	278	29	72
East	24	2347	245	19	1083	358	328	28	0	287	59	78	93	0	2167	331	516	0	0	2537	152	523
West	24	2482	106	9	537	154	133	14	0	83	22	24	19	0	833	131	212	37	0	1620	212	389
Muddy Mtn	21	2339	65	9	509	109	127	0	0	65	11	17	28	0	546	104	150	0	0	306	35	79
Medicine Bow Mtns																						
South	24	2633	74	0	389	107	103	14	0	2926	222	652	9	0	3769	321	812	0	0	481	37	103
North	24	2797	74	0	417	107	107	9	0	4444	226	901	37	0	907	137	247	19	0	1167	120	254
Sierra Madre	24	2736	65	0	361	91	89	0	0	130	14	30	5	0	2528	220	534	5	0	861	61	179
Sweetwater Basin																						
Shirley Mtns	24	2424	97	28	1935	250	436	0	0	46	4	12	0	0	0	0	0	0	0	37	2	8
Ferris Mtns	6	2293	65	0	454	116	171	0	0	19	6	10	0	0	0	0	0	14	0	28	14	13
Green Mtns	24	2516	148	19	806	242	232	0	0	278	31	73	0	0	315	39	91	0	0	0	0	0
Beaver Divide	16	2287	79	56	213	106	51	0	0	19	2	5	0	0	944	76	242	0	0	0	0	0
Wind River Range																						
South	27	2599	130	0	565	135	125	0	0	333	30	68	0	0	833	139	248	0	0	37	4	10
Reservation	18	2654	60	0	583	124	160	0	0	37	6	10	5	0	833	107	234	5	0	685	80	172
North	28	2503	56	0	361	103	105	0	0	324	30	74	0	0	1102	109	262	32	0	4787	289	903
Absaroka Range																						
South	20	2462	23	0	148	36	45	0	0	83	12	23	0	0	1380	182	342	23	0	1120	181	323
Shoshone Canyon	17	2083	139	9	426	161	114	65	0	194	66	64	0	0	0	0	0	0	0	148	29	46
North	24	2054	5	0	333	54	93	0	0	111	10	24	0	0	0	0	0	0	0	352	25	75
Bighorn Basin	11	1918	37	0	380	88	120	19	0	157	34	47	0	0	0	0	0	0	0	28	6	10
Bighorn Mtns																						
East	17	2404	83	37	463	135	116	0	0	231	21	58	0	0	0	0	0	46	0	1352	161	326
South	20	2518	42	0	176	56	49	0	0	1407	129	382	0	0	315	16	70	28	0	315	52	69
North	24	2478	19	0	407	65	97	0	0	463	35	94	0	0	167	19	46	51	0	1241	121	259
Montana																						
Pryor Mtns	20	2076	32	0	333	67	83	0	0	370	48	99	0	0	0	0	0	46	0	861	141	216
Terry Badlands	8	858	60	9	148	80	59	28	0	83	36	32	0	0	0	0	0	0	0	0	0	0
	508	2376	74	0	1935	141	201	0	0	4444	64	274	0	0	3806	136	370	0	0	4787	83	300

[a]One plot consists of three 60 x 6 m subplots placed at random bearings with a 30 x 6 m invasive species and white pine blister rust alternate host plot at the end of each subplot.
[b]Other pines include ponderosa pine, lodgepole pine, whitebark pine, Rocky Mountain juniper, and Utah juniper.
[c]Spruce-fir includes Engelmann spruce, white spruce, Douglas-fir, and subalpine fir.

Table 2.2: Live limber pine seedling density (stems/ha) (n = 508 plots) in three height classes in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

State, geographic range, and study area	0-45.7 cm					45.7-91.4 cm					91.4-137 cm				
	median	min	max	mean	std	median	min	max	mean	std	median	min	max	mean	std
Colorado															
Front Range															
Boulder County	19	0	630	116	217	19	0	259	51	81	14	0	130	26	36
North	19	0	444	51	95	19	0	93	27	28	19	0	93	19	19
Wyoming															
Laramie Mtns															
Pole Mtn	125	19	1213	189	243	130	0	324	126	94	46	0	157	58	42
East	51	0	917	185	277	97	0	306	112	85	46	0	194	61	50
West	42	0	269	66	76	42	0	194	54	50	28	0	102	33	28
Muddy Mtn	9	0	315	37	76	19	0	167	39	43	19	0	120	32	33
Medicine Bow Mtns															
South	14	0	296	39	74	37	0	111	37	29	19	0	111	31	27
North	23	0	157	39	43	28	0	194	40	47	19	0	102	29	33
Sierra Madre	19	0	102	25	30	23	0	176	35	40	19	0	157	30	36
Sweetwater Basin															
Shirley Mtns	9	0	546	60	136	37	0	1019	112	225	37	9	500	78	116
Ferris Mtns	9	0	157	34	62	14	0	204	51	80	28	0	93	31	34
Green Mtns	32	0	537	76	124	74	0	398	104	99	42	9	250	61	59
Beaver Divide	9	0	74	19	22	37	9	111	42	27	32	0	102	46	34
Wind River Range															
South	37	0	333	54	69	28	0	148	50	41	19	0	120	31	32
Reservation	9	0	306	47	79	28	0	259	52	73	9	0	111	25	29
North	14	0	194	30	49	28	0	157	40	43	28	0	148	32	31
Absaroka Range															
South	0	0	56	11	19	9	0	65	14	18	9	0	56	11	14
Shoshone Canyon	46	0	222	69	67	65	0	204	58	54	28	9	65	34	20
North	0	0	185	19	48	0	0	185	20	44	0	0	56	15	21
Bighorn Basin	0	0	102	26	36	0	0	176	31	55	19	0	130	31	39
Bighorn Mtns															
East	19	0	296	44	73	37	9	194	57	48	28	0	111	35	31
South	5	0	56	14	18	9	0	93	22	26	9	0	83	20	24
North	0	0	46	12	17	9	0	176	29	47	9	0	204	24	42
Montana															
Pryor Mtns	9	0	130	19	31	19	0	111	23	30	9	0	93	25	30
Terry Badlands	37	0	93	39	29	19	0	83	23	27	5	0	93	17	31
	19	0	1213	55	117	28	0	1019	52	78	19	0	500	34	44

Table 2.3: Linear regression for density (stems/ha) of limber pine seedlings, proportion of limber pine seedlings with WPBR, and terminal growth (mm) of limber pine seedlings from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

Model[a]	Parameter	Estimate	Standard error
Log_{10} stems/ha of limber pine seedlings	Intercept	1.0424	0.1246
	Log_{10} stems/ha of limber pine trees	0.2943	0.0376
	Log_{10} stems/ha of all live trees	0.2304	0.0412
	Grass (percent cover)	-0.0026	0.0009
	Limber pine seedling height (cm)	-0.0043	0.0005
Square root (Proportion of limber pine seedlings with WPBR) with canker data	Intercept	-0.0612	0.0269
	Limber pine seedling height (cm)	0.0012	0.0003
	Log_{10} tree cankers/ha	0.0520	0.0070
Square root (Proportion of limber pine seedlings with WPBR) without canker data	Intercept	-0.0804	0.0287
	Limber pine seedling height (cm)	0.0013	0.0003
	Crown dieback (percent)	0.0009	0.0003
	Log_{10} stems/ha of trees with WPBR	0.0590	0.0090
Terminal growth (mm) of limber pine seedlings	Intercept	8.8870	2.5138
	Log basal area (m^2/ha) of all live mature trees	-8.3331	1.6224
	Big sagebrush (percent of total ground cover)	0.3163	0.0511
	Limber pine seedling height (cm)	0.4491	0.0218
	Grass as seedling ground cover	11.7085	1.5455

[a]Model fit using SAS Proc Mixed with study area as a random effect.

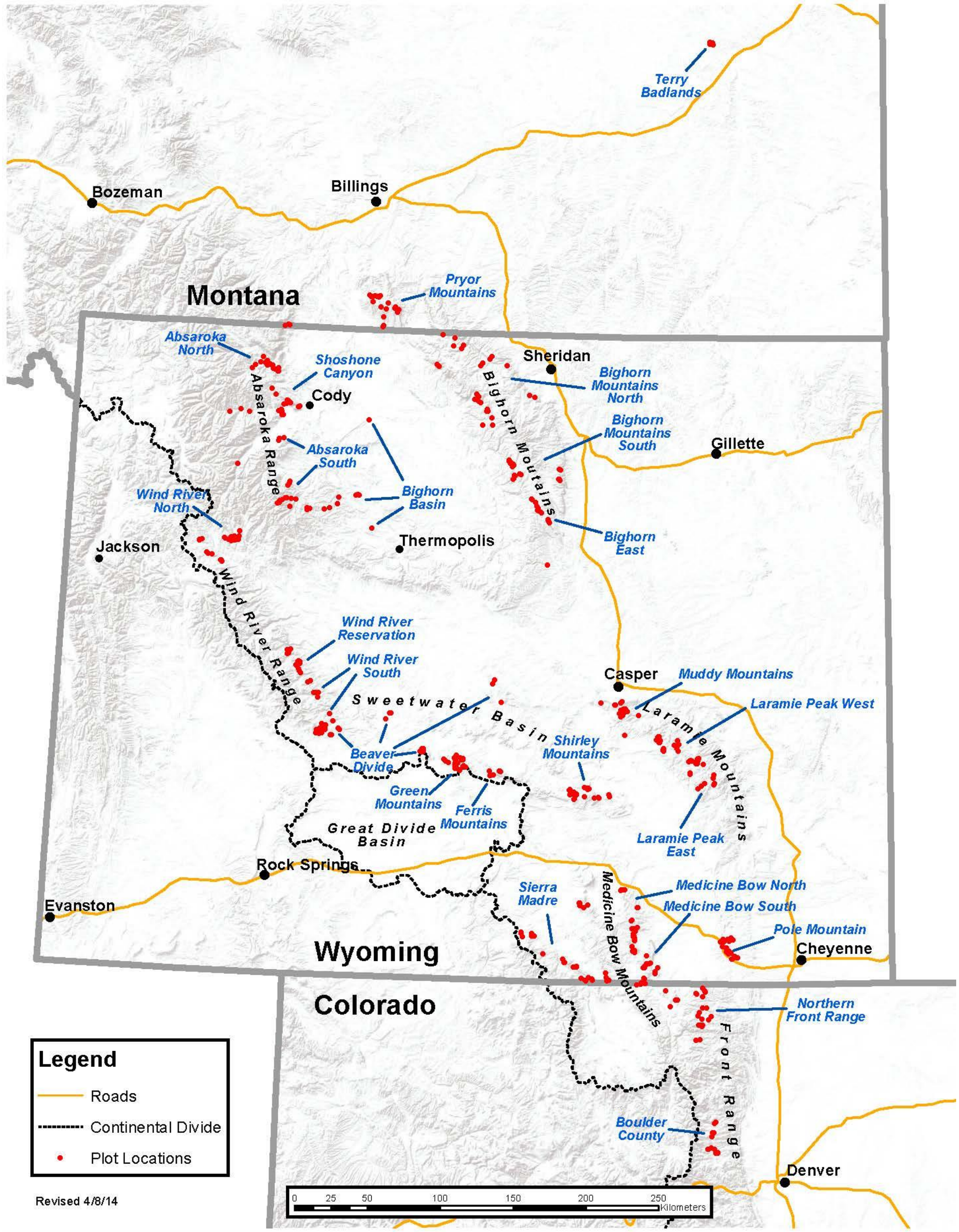


Figure 2.1: Location of limber pine monitoring plots in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

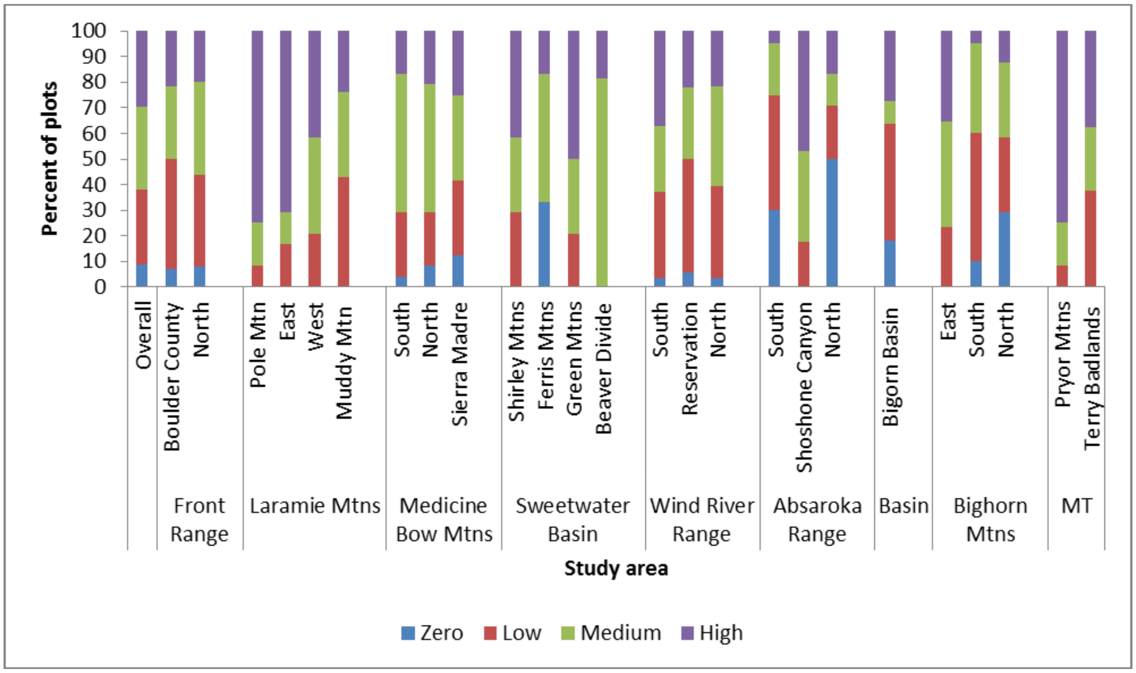
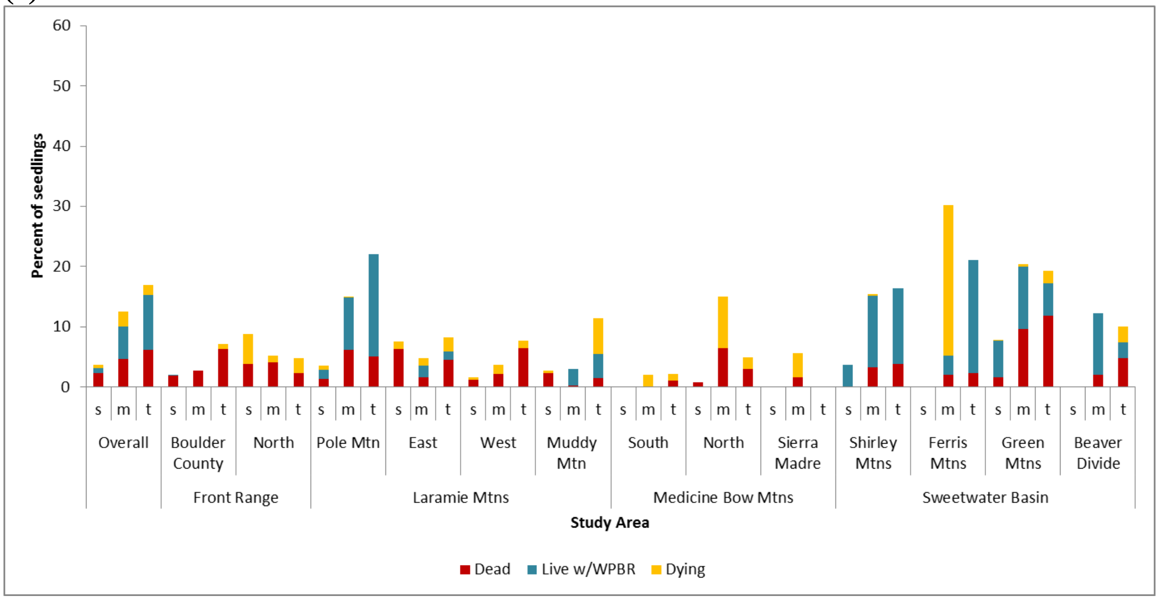


Figure 2.2: Percent of plots in live limber pine seedling density classes (zero: no seedlings, low: >0 – 55 stems/ha, medium: >55 – 140 stems/ha, and high: >140 stems/ha) in Colorado, Wyoming, and Montana in 2011 and 2012.

(a)



(b)

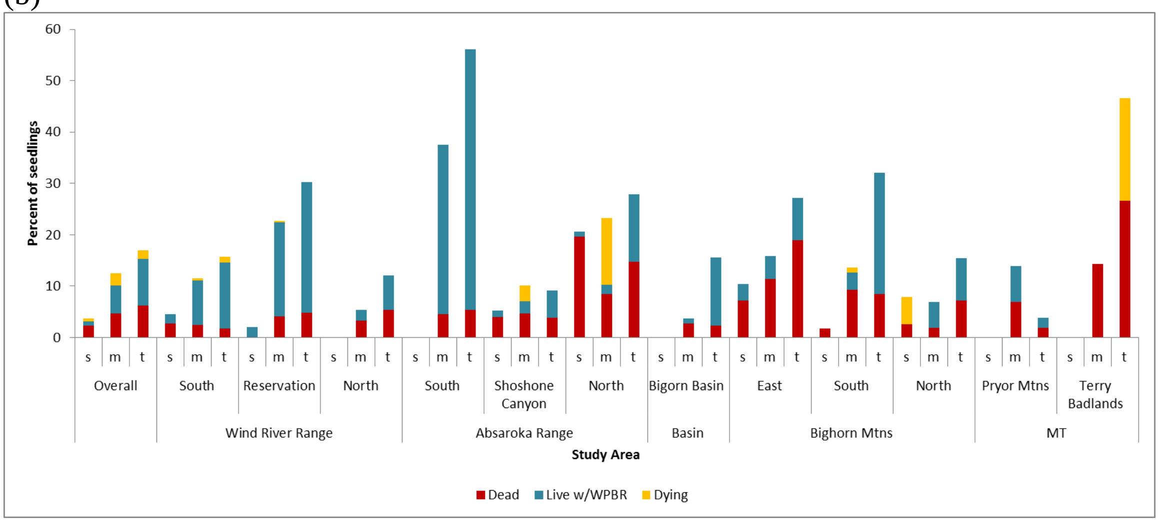
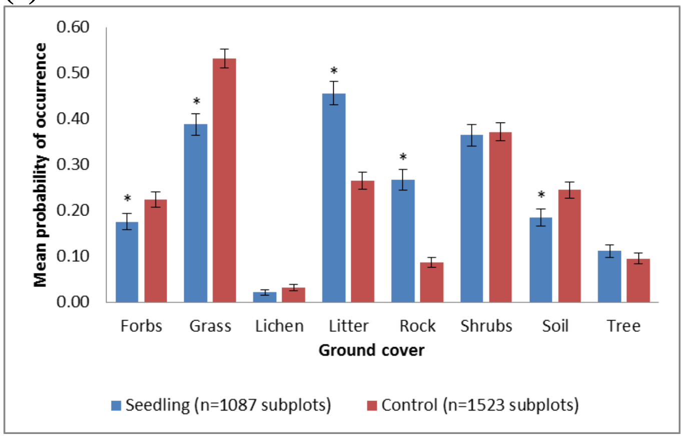


Figure 2.3: Percent of limber pine seedlings that were dead, live and infected with WPBR, and live but dying (>50% of crown showing symptoms or is damaged; excludes dying with WPBR) in three height classes (s: small 0-45.7 cm, m: medium >45.7-91.4 cm, and t: tall >91.4-137 cm) in the (a) southern Rocky Mountains and (b) central Rocky Mountains from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

(a)



(b)

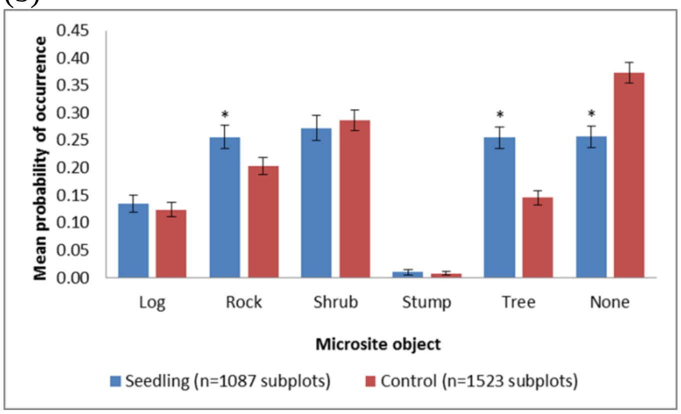
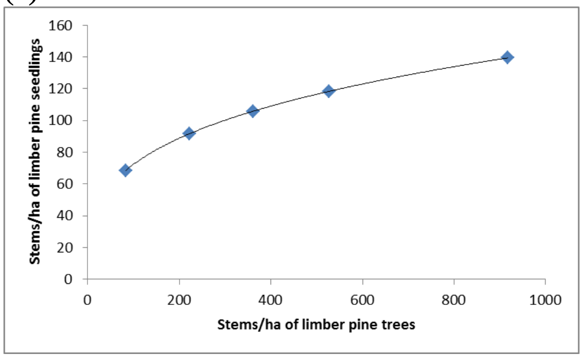
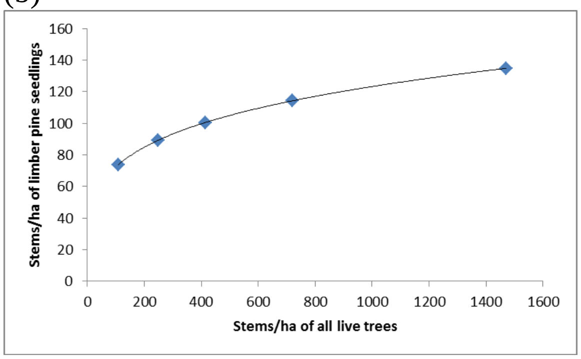


Figure 2.4: Mean probability of occurrence of (a) ground cover type and (b) microsite object type within one meter of a limber pine seedling as compared to the same within one meter of a control point (each subplot contained two fixed control points located at the subplot midpoint, three meters from each end) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Error bars represent standard error of the mean. Comparisons between seedling and control point means were made using a paired t-test with the critical level of significance set as $P < 0.0001$ (as indicated by an asterisk).

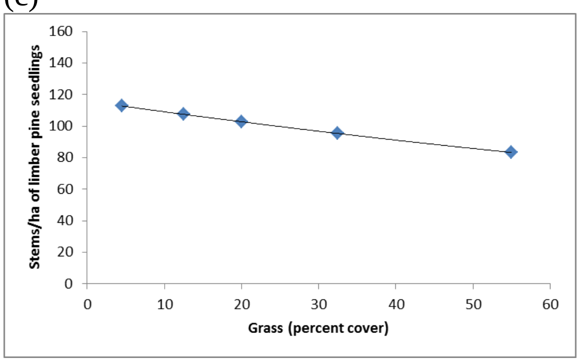
(a)



(b)



(c)



(d)

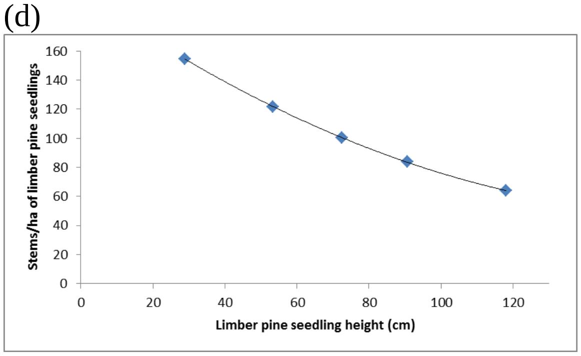
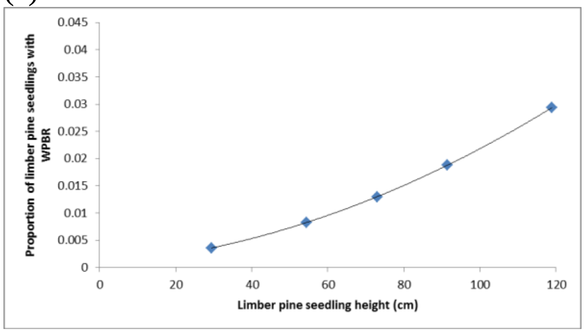


Figure 2.5: Linear regression analysis predicting density (stems/ha) of limber pine seedlings on a subplot using variables selected in the final model (fit using PROC MIXED with study area as a random effect, in SAS) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Relationship with response variable was plotted using mean values and the 5th, 25th, 50th, 75th, and 95th percentiles. Predicted values were

back transformed. Positive relationships exist between (a) stems/ha of limber pine seedlings and stems/ha of limber pine trees and (b) stems/ha of all live trees. Negative relationships exist between (c) stems/ha of limber pine seedlings and grass (percent cover) and (d) limber pine seedling height (cm).

(a)



(b)

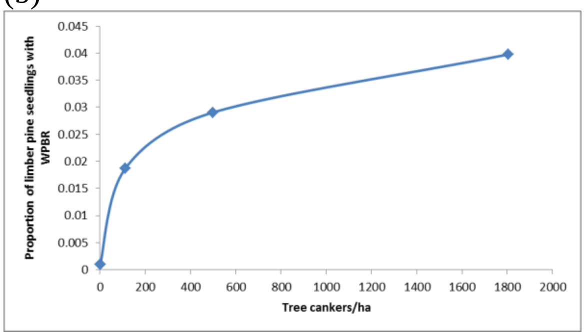


Figure 2.6: Linear regression analysis predicting proportion of limber pine seedlings infected with WPBR on a subplot using variables selected in the final model (fit using PROC MIXED with study area as a random effect, in SAS) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Relationship with response variable was plotted using mean values and the 5th, 25th, 50th, 75th, and 95th percentiles. Predicted values were back transformed. Positive relationships exist between (a) proportion of limber pine seedlings with WPBR and limber pine seedling height (cm) and (b) tree cankers/ha.

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Appendix I: Method Details

Steps to extract Daymet data for Limber Pine Plots:

1. Downloaded Daymet Daily Surface Gridded Data in NetCDF format from this site:

http://daymet.ornl.gov/gridded

For each of these tile ID's: 11737, 11738, 11916, 11917, 11918, 12096, 12097, 12278

and for years 2000 to 2012.

2. Run R script called Process_Daymet_Jacobi.R to extract tmax, tmin, precip, and vaporpressure values from NetCDF by tile by year.

3. Run R script called Process_Daymet_Jacobi_GETPOINTS_ONLY.R (see code in appendix) to get only Dayment x/y coordinates and with unique ID.

4. Run ArcMap "nearest point" spatial join between results of step 3 and Limber Pine plot points to get Daymet ID and Limber Pine plot ID cross reference list.

5. Run R script called Calc_Monthly_Totals_Jacobi.R (see code in appendix) to get monthly and yearly totals for all Daymet data nearest Limberpine plots.

6. Run R script called Append_Create_Cols_Jacobi.R (see code in appendix) to merge data into one file, then perform cross-tabulation to put all values in columns with one row for each Limber Pine Plot.

7. Converted results of Step 6 to Excel Spreadsheet and delivered to Jacobi.

Appendix II: Additional Tables and Figures

Table 2.4: Dispersal of limber pine seedlings across three height categories (s: small 0-45.7 cm, m: medium 45.7-91.4 cm, and t: tall 91.4-137 cm) in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

State, geographic range, and study area	Percent of limber pine seedlings			
	Not present	1 height category	2 height categories	All height categories
Colorado				
Front Range				
Boulder County	7	7	14	71
North	8	20	8	64
Wyoming				
Laramie Mtns				
Pole Mtn	0	0	8	92
East	0	4	17	79
West	0	8	17	75
Muddy Mtn	0	24	29	48
Medicine Bow Mtns				
South	4	0	38	58
North	8	17	21	54
Sierra Madre	13	4	33	50
Sweetwater Basin				
Shirley Mtns	0	4	42	54
Ferris Mtns	33	0	17	50
Green Mtns	0	0	25	75
Beaver Divide	0	6	25	69
Wind River Range				
South	4	4	26	67
Wind River Res	6	17	11	67
North	4	18	21	57
Absaroka Range				
South	30	25	20	25
Shoshone Canyon	0	6	12	82
North	50	21	13	17
Bighorn Basin	18	27	18	36
Bighorn Mtns				
East	0	0	35	65
South	10	15	50	25
North	29	13	21	38
Montana				
Pryor Mtns	10	30	20	40
Terry Badlands	0	25	38	38
	9	11	23	57

Table 2.5: Mean height of seedlings (<137 cm) in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

	Height (cm)							
State, geographic	Limber		Other Pine		Aspen		Spruce-fir	
range, and study area	mean	std	mean	std	mean	std	mean	std
Colorado								
Front Range								
Boulder County	50.3	17.3	63.3	13.2	54.5	8.0	37.0	18.8
North	66.2	27.5	70.3	25.6	70.2	14.3	60.7	26.2
Wyoming								
Laramie Mtns								
Pole Mtn	57.0	12.7	64.0	21.9	70.9	15.0	62.5	34.2
East	66.9	22.6	69.0	26.3	60.5	16.2	61.0	19.9
West	67.2	19.9	80.2	21.5	52.5	13.3	62.4	11.8
Muddy Mtn	78.4	25.6	72.9	27.9	70.0	12.7	65.5	28.4
Medicine Bow Mtns								
South	74.4	18.2	67.9	29.4	68.7	23.0	47.3	37.4
North	64.1	19.3	64.4	18.9	74.2	18.4	64.2	22.7
Sierra Madre	74.7	17.9	66.7	21.2	81.3	18.5	57.6	31.0
Sweetwater Basin								
Shirley Mtns	85.8	19.3	95.2	46.2	.	.	74.2	35.0
Ferris Mtns	76.5	12.2	74.0	.	.	.	75.8	42.2
Green Mtns	75.5	18.6	75.7	23.1	50.1	12.7	.	.
Beaver Divide	82.3	13.4	69.3	40.0	62.3	33.5	.	.
Wind River Range								
South	65.6	16.3	73.4	30.5	69.5	14.2	79.4	25.4
Reservation	75.5	22.3	78.7	41.8	70.3	20.3	87.9	30.7
North	77.6	23.3	77.3	22.7	76.8	18.0	71.5	28.7
Absaroka Range								
South	78.3	21.9	82.0	28.0	63.3	13.4	63.3	19.9
Shoshone Canyon	68.9	21.0	66.7	26.4	.	.	59.9	28.8
North	78.8	30.8	77.0	31.6	.	.	83.6	30.9
Bighorn Basin	82.9	27.6	89.8	25.7	.	.	86.2	18.8
Bighorn Mtns								
East	71.5	18.2	74.1	28.8	.	.	72.9	22.6
South	79.8	25.7	89.4	34.1	88.1	.	78.6	18.2
North	86.3	19.7	73.3	21.8	45.7	14.9	68.4	21.6
Montana								
Pryor Mtns	73.2	24.5	73.8	29.2	.	.	65.6	17.2
Terry Badlands	58.6	17.3	81.6	13.4	.	.	.	.
	72.5	22.1	72.9	25.7	66.8	17.9	66.8	26.0

Table 2.6: Seedling health status in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Values are percent of seedlings in each health status category. Healthy = no visual damage to crown or stem up to 5% damage, declining/dying = 6-50% of crown showing symptoms that indicates it is dead or will be or >50% of crown showing symptoms or is damaged, dead = recent dead (no green needles, red needles but fines still present), old dead (no fine twigs, no needles, >50% bark still present), very old dead (no fine twigs, no needles, <50% of bark present). Means are based on plot means.

State, geographic range, and study area	Limber pine			Other pine			Aspen			Spruce-fir		
	Healthy	Declining/ dying	Dead	Healthy	Declining/ dying	Dead	Healthy	Declining/ dying	Dead	Healthy	Declining/ dying	Dead
Colorado												
Front Range												
Boulder County	91	7	2	88	10	2	84	6	10	99	0	0
North	90	7	3	93	6	1	85	5	9	100	0	0
Wyoming												
Laramie Mtns												
Pole Mtn	89	7	3	92	5	3	74	9	17	98	2	0
East	87	10	3	86	12	2	65	20	15	94	1	5
West	93	4	3	92	5	3	77	9	15	100	0	0
Muddy Mtn	93	6	1	88	13	0	89	6	4	99	1	0
Medicine Bow Mtns												
South	86	13	0	94	5	1	85	2	12	95	5	0
North	86	11	3	94	5	1	86	8	6	100	0	0
Sierra Madre	96	4	1	93	4	3	89	8	3	99	0	1
Sweetwater Basin												
Shirley Mtns	83	13	4	100	0	0	-	-	-	100	0	0
Ferris Mtns	61	38	1	100	0	0	-	-	-	83	17	0
Green Mtns	76	14	10	95	4	0	77	8	15	-	-	-
Beaver Divide	85	12	3	100	0	0	92	5	3	-	-	-
Wind River Range												
South	85	13	2	96	4	0	87	7	6	100	0	0
Wind River Res	79	16	5	100	0	0	78	16	6	94	5	1
North	91	4	4	99	1	0	84	5	10	96	4	0
Absaroka Range												
South	65	32	3	100	0	0	83	10	7	95	1	5
Shoshone Canyon	88	9	3	99	1	0	-	-	-	96	2	3
North	66	22	13	99	1	0	-	-	-	88	0	12
Bighorn Basin	83	14	3	99	1	0	-	-	-	100	0	0
Bighorn Mtns												
East	83	6	11	95	0	5	-	-	-	100	0	0
South	77	14	9	100	0	0	87	3	11	99	1	0
North	87	5	7	97	2	0	97	3	0	95	4	1
Montana												
Pryor Mtns	85	12	3	97	3	0	-	-	-	100	0	0
Terry Badlands	91	3	6	93	7	0	-	-	-	-	-	-
	85	11	4	94	5	1	82	8	10	97	2	1

Table 2.7: Health status of limber pine seedlings in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Means are based on overall seedling means.

State, geographic range, and study area	Health status of limber pine seedlings (percent)							Health status of limber pine seedlings <70 cm tall (percent)							Health Status of limber pine seedlings ≥70 cm tall (percent)						
	n[a]	1[b]	2[c]	3[d]	4[e]	5[f]	6[g]	n	1	2	3	4	5	6	n	1	2	3	4	5	6
Colorado																					
Front Range																					
Boulder County	307	81.1	14.0	0.3	2.9	1.6	0.0	235	85.1	11.5	0.0	2.1	1.3	0.0	72	68.1	22.2	1.4	5.6	2.8	0.0
North	267	90.6	5.6	1.1	1.9	0.7	0.0	177	92.1	5.1	0.6	1.7	0.6	0.0	90	87.8	6.7	2.2	2.2	1.1	0.0
Wyoming																					
Laramie Mtns																					
Pole Mtn	999	89.5	5.5	1.7	1.4	1.9	0.0	691	92.5	4.2	1.0	1.0	1.3	0.0	308	82.8	8.4	3.2	2.3	3.2	0.0
East	962	90.1	4.9	1.6	1.9	1.5	0.1	673	92.1	3.1	1.6	2.1	0.9	0.1	289	85.5	9.0	1.4	1.4	2.8	0.0
West	409	90.5	5.4	1.5	1.0	1.7	0.0	254	93.7	3.1	1.2	0.4	1.6	0.0	155	85.2	9.0	1.9	1.9	1.9	0.0
Muddy Mtn	253	91.7	5.1	0.8	2.4	0.0	0.0	131	94.7	2.3	0.8	2.3	0.0	0.0	122	88.5	8.2	0.8	2.5	0.0	0.0
Medicine Bow Mtns																					
South	279	91.0	7.5	1.1	0.0	0.4	0.0	153	96.1	2.6	1.3	0.0	0.0	0.0	126	84.9	13.5	0.8	0.0	0.8	0.0
North	283	87.6	8.5	1.8	1.1	1.1	0.0	162	88.3	8.6	1.2	1.2	0.6	0.0	121	86.8	8.3	2.5	0.8	1.7	0.0
Sierra Madre	238	96.2	1.7	1.7	0.0	0.4	0.0	101	99.0	1.0	0.0	0.0	0.0	0.0	137	94.2	2.2	2.9	0.0	0.7	0.0
Sweetwater Basin																					
Shirley Mtns	658	93.3	4.0	1.1	0.8	0.9	0.0	300	95.0	3.3	0.3	1.0	0.3	0.0	358	91.9	4.5	1.7	0.6	1.4	0.0
Ferris Mtns	78	71.8	23.1	1.3	1.3	2.6	0.0	40	77.5	20.0	0.0	2.5	0.0	0.0	38	65.8	26.3	2.6	0.0	5.3	0.0
Green Mtns	669	81.2	9.9	2.5	2.1	4.3	0.0	357	89.6	4.2	2.0	1.1	3.1	0.0	312	71.5	16.3	3.2	3.2	5.8	0.0
Beaver Divide	188	85.1	10.1	2.1	1.1	1.1	0.5	67	94.0	4.5	1.5	0.0	0.0	0.0	121	80.2	13.2	2.5	1.7	1.7	0.8
Wind River Range																					
South	401	87.0	9.5	1.5	1.2	0.7	0.0	246	92.7	4.9	0.8	0.8	0.8	0.0	155	78.1	16.8	2.6	1.9	0.6	0.0
Wind River Res	248	79.8	16.5	1.2	1.2	1.2	0.0	145	85.5	13.1	0.7	0.7	0.0	0.0	103	71.8	21.4	1.9	1.9	2.9	0.0
North	319	93.1	3.8	0.6	0.6	0.9	0.9	157	97.5	1.9	0.6	0.0	0.0	0.0	162	88.9	5.6	0.6	1.2	1.9	1.9
Absaroka Range																					
South	81	70.4	18.5	7.4	1.2	0.0	2.5	35	91.4	8.6	0.0	0.0	0.0	0.0	46	54.3	26.1	13.0	2.2	0.0	4.3
Shoshone Canyon	308	87.0	7.8	1.3	1.9	0.3	1.6	192	92.2	4.7	0.0	1.6	0.0	1.6	116	78.4	12.9	3.4	2.6	0.9	1.7
North	160	81.3	3.8	3.1	1.9	3.1	6.9	90	87.8	1.1	2.2	2.2	3.3	3.3	70	72.9	7.1	4.3	1.4	2.9	11.4
Bighorn Basin	109	90.8	4.6	0.9	1.8	0.0	1.8	52	92.3	3.8	0.0	0.0	0.0	3.8	57	89.5	5.3	1.8	3.5	0.0	0.0
Bighorn Mtns																					
East	271	85.6	3.3	2.6	4.4	3.3	0.7	133	91.7	2.3	1.5	3.0	1.5	0.0	138	79.7	4.3	3.6	5.8	5.1	1.4
South	130	83.8	6.2	3.1	3.1	3.1	0.8	58	91.4	3.4	0.0	3.4	1.7	0.0	72	77.8	8.3	5.6	2.8	4.2	1.4
North	173	90.8	5.2	1.2	0.0	1.2	1.7	71	93.0	1.4	2.8	0.0	1.4	1.4	102	89.2	7.8	0.0	0.0	1.0	2.0
Montana																					
Pryor Mtns	147	90.5	7.5	0.0	0.7	0.0	1.4	73	93.2	5.5	0.0	0.0	0.0	1.4	74	87.8	9.5	0.0	1.4	0.0	1.4
Terry Badlands	72	94.4	0.0	1.4	0.0	1.4	2.8	45	100.0	0.0	0.0	0.0	0.0	0.0	27	85.2	0.0	3.7	0.0	3.7	7.4
	8009	87.0	7.7	1.7	1.4	1.3	0.9	4638	91.9	5.0	0.8	1.1	0.7	0.5	3371	81.1	10.9	2.7	1.9	2.1	1.3

[a]Number of stems
[b]Health status = 1, no visual damage to crown or stem up to 5% damage.
[c]Health status = 2, declining, 6-50% of crown showing symptoms that indicates it is dead or will be.
[d]Health status = 3, dying, >50% of crown showing symptoms or is damaged.
[e]Health status = 4, recent dead, no green needles, red needles but fines still present.
[f]Health status = 5, old dead, no fine twigs, no needles, >50% bark still present.
[g]Health status = 6, very old dead, no fine twigs, no needles, <50% of bark present.

Table 2.8: Using logistic regression analysis predicting limber pine seedling occurrence (y/n) on a subplot, these variables (presented with means, standard deviations, Wilcoxon two-sided p-values, and noted if selected for the final model) were selected in at least 20 percent of 1000 models after screening each category using PROC GLMSELECT from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Stand structure is a categorical variable.

		Limber pine seedling occurrence							
		no			**yes**			**Wilcoxon**	
Category	**Variable**	**n**	**mean**	**std**	**n**	**mean**	**std**	**Two-sided Pr>|Z|**	**final model**
Plot	stand structure (cc: closed canopy):	-	-	-	-	-	-	-	
	cc multistory	10	2.29	-	43	3.96	-	-	
	cc multistory with open individuals and/or open scattered clumps	24	5.49	-	150	13.80	-	-	
	cc single story with open individuals and/or open scattered clumps (includes mosaic of closed canopy single and multistory).	120	27.46	-	224	20.61	-	-	
	open canopy, scattered individuals and/or scattered clumps	283	64.76	-	670	61.64	-	-	
	northing	437	4788973	1.70	1087	47.24	1.54	<0.0001	
Trees	$\log_{10}$ basal area (m²/ha) of limber pine trees with bark beetles	437	0.37	0.49	1087	0.41	0.52	0.0965	
	proportion of basal area (m²/ha) of limber pine trees	434	0.75	0.34	1085	0.76	0.32	0.3845	yes
	$\log_{10}$ stems/ha all live trees	427	2.51	0.36	1078	2.66	0.35	<0.0001	yes
	$\log_{10}$ basal area (m²/ha) all live trees	427	0.76	0.55	1078	0.75	0.54	0.5012	
Ground cover	√percent of *Ribes inerme*	436	0.19	0.72	1087	0.05	0.35	<0.0001	
	grass (percent cover)	436	26.67	17.37	1087	22.54	14.54	<0.0001	
Meteorological	relative humidity in January	437	58.58	4.89	1087	60.67	5.59	<0.0001	
	frost days	437	8339	1994	1087	7128	3517	0.0826	

Table 2.9: Using linear regression analysis predicting limber pine seedling density (stems/ha) on a subplot (n), these variables [presented with means, standard deviations, Pearson correlation coefficients (P), and noted if selected for the final model] were selected in at least 20 percent of 1000 models after screening each category using PROC GLMSELECT from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Aspect and stand structure are categorical variables.

Category	**Variable**	**n**	**mean**	**std**	**PCC**	**p-value**	**final model**
Plot	aspect:	1524					
	east	316	1.35	1.01	-	-	
	south	458	1.38	0.99	-	-	
	west	418	1.49	1.02	-	-	
	north	332	1.69	0.98	-	-	
	stand structure (cc: closed canopy):	1524					
	cc multistory	53	1.72	0.94	-	-	
	cc multistory with open individuals and/or open scattered clumps	174	1.88	0.89	-	-	
	cc single story with open individuals and/or open scattered clumps (includes mosaic of cc single and multistory)	344	1.36	1.06	-	-	
	open canopy, scattered individuals and/or scattered clumps	953	1.42	0.99	-	-	
	northing	1524	4742698	1.62	-0.19	<0.0001	
Ground cover	grass (percent cover)	1523	23.72	15.51	-0.14	<0.0001	yes
Trees	$\log_{10}$ basal area (m^2/ha) of limber pine	1524	0.90	0.41	0.04	0.1266	
	$\log_{10}$ basal area (m^2/ha) of all live trees	1505	0.75	0.54	0.03	0.3103	
	$\log_{10}$ stems/ha of limber pine	1524	2.48	0.45	0.30	<0.0001	yes
	$\log_{10}$ stems/ha of all live trees	1505	2.62	0.36	0.27	<0.0001	yes
	$\log_{10}$ stems/ha of aspen	1524	0.42	0.90	0.15	<0.0001	
	$\log_{10}$ stems/ha spruce-fir	1524	0.75	1.04	-0.08	0.0014	
	proportion of limber pine in the intermediate crown class	1499	32.60	27.03	0.21	<0.0001	
Seedlings	$\log_{10}$ stems/ha of other pine seedlings	1524	0.60	0.94	0.19	<0.0001	
	$\log_{10}$ stems/ha of aspen seedlings	1524	0.53	1.07	0.18	<0.0001	
	limber pine seedling height (cm)	1087	72.43	26.89	-0.27	<0.0001	yes
	shrub as seedling microsite object	1087	0.27	0.38	-0.16	<0.0001	
	shrubs as seedling ground cover	1087	0.36	0.39	-0.15	<0.0001	
Meteorological	frost days	1524	7475	3203	-0.16	<0.0001	

Table 2.10. Using linear regression analysis predicting proportion of limber pine seedlings infected with WPBR on a subplot, these variables (presented with means, standard deviations, Pearson correlation coefficients (P), and noted if selected for the final model) were selected in at least 20 percent of the models after screening each category using PROC GLMSELECT from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Slope position is a categorical variable.

Category	**Variable**	**n**	**mean**	**std**	**PCC**	**p-value**	**final model**
Plot	northing	1386	4754135	1.43	0.09	0.0051	
	grazing as historical disturbance	1386	0.67	0.47	0.14	<0.0001	
	slope position:						
	backslope	397	0.13	0.27	-	-	
	footslope	158	0.11	0.23	-	-	
	shoulder	294	0.10	0.22	-	-	
	summit	140	0.09	0.23	-	-	
Ground cover	litter (percent cover)	1385	12.94	12.59	-0.10	0.001	
	tree/log (percent cover)	1385	7.44	7.53	-0.11	0.0006	
	grass (percent cover)	1385	23.89	15.41	0.09	0.0041	
Trees	$\log_{10}$ basal area (m^2/ha) of all live trees	1368	0.75	0.55	-0.07	0.0366	
	crown dieback (percent)	1361	28.95	27.59	0.08	0.0107	
	$\log_{10}$ tree cankers/ha	1333	1.62	1.27	0.34	<0.0001	yes
Seedlings	limber pine height (cm)	988	73.14	26.71	0.15	<0.0001	yes
	grass as seedling ground cover	988	0.40	0.39	0.14	<0.0001	
Meteorological	relative humidity in October	1386	51.55	3.11	0.17	<0.0001	
	relative humidity in April	1386	58.08	2.18	0.16	<0.0001	
	drought frequency1	1386	15.98	2.18	-0.16	<0.0001	
	relative humidity in November	1386	61.62	3.86	0.16	<0.0001	

Table 2.11: Using linear regression analysis predicting limber pine seedling terminal growth (mm) on a subplot, these variables (presented with means, standard deviations, Pearson correlation coefficients (P), and noted if selected for the final model) were selected in at least 20 percent of 1000 models after screening each category using PROC GLMSELECT from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Slope position is categorical.

Category	Variable	n	mean	std	PCC	p-value	final model
Plot	northing	1524	4742698	1.62	0.13	<0.0001	
	grazing as a historical disturbance	1524	0.66	0.47	0.21	<0.0001	
	slope position:						
	backslope	410	38.39	20.86	-	-	
	footslope (includes toeslope and valley bottom)	169	52.57	30.13	-	-	
	shoulder	328	38.21	23.54	-	-	
	summit	152	43.43	23.45	-	-	
Ground cover	litter (percent cover)	1523	13.43	13.32	-0.33	<0.0001	
	rock (percent cover)	1523	10.53	11.66	-0.21	<0.0001	
	grass (percent cover)	1523	23.72	15.51	0.27	<0.0001	
	shrubs (percent cover)	1523	18.81	14.58	0.24	<0.0001	
	big sagebrush (percent of shrub cover)	1523	9.15	11.79	0.30	<0.0001	yes
Seedlings	limber pine seedling height (cm)	1087	72.43	26.89	0.58	<0.0001	yes
	shrub as a seedling microsite object	1087	0.27	0.38	0.20	<0.0001	
	grass as dominant groundcover next to seedling	1087	0.39	0.39	0.32	<0.0001	yes
	litter as dominant groundcover next to seedling	1087	0.46	0.41	-0.31	<0.0001	
	$\log_{10}$ stems/ha of all other seedlings	1524	1.27	1.23	-0.25	<0.0001	
Metorological	mean August preciptitation (derived from 30-year (1971-2000) normals)	1524	13.04	2.95	-0.24	<0.0001	
	seasonal (April-Sept) moisture index	1524	1397.00	343.13	0.23	<0.0001	
	avg max temp July-Sept for 2010 and 2011	1524	22.18	1.87	0.11	0.0004	
	avg min temp July-Sept for 2009 and 2010	1524	6.23	1.41	0.10	0.0011	
Trees	$\log_{10}$ basal area (m^2/ha) all live trees	1505	0.87	0.38	-0.23	<0.0001	yes
	$\log_{10}$ basal area (m^2/ha) of limber pine trees with WPBR	1524	0.33	0.40	0.15	<0.0001	
	$\log_{10}$ basal area (m^2/ha) of other pine trees	1524	0.29	0.46	-0.29	<0.0001	
	$\log_{10}$ basal area (m^2/ha) of spruce-fir trees	1524	0.17	0.35	-0.16	<0.0001	
	$\log_{10}$ stems/ha of limber pine trees with WPBR	1500	1.34	1.13	0.13	<0.0001	

Table 2.12: Site (plot), ground cover, and WPBR alternate host variables used during statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

Site (plot) variables		**Ground cover variables**	**WPBR alternate host variables**
	Northing (latituide)	Soil (percent cover)	Stream density within 1 km
	Elevation (m)	Litter (percent cover)	Area (m²) occupied by *Ribes* spp.
Aspect	North	Rock (percent cover)	Area (m²) occupied by *Castilleja* spp.
	South	Tree/log (percent cover)	
	East	Lichens/moss (percent cover)	
	West	Grass (percent cover)	
	Slope (percent)	Forbs (percent cover)	
Slope position	Summit	Shrubs (percent cover)	
	Shoulder	Common juniper (percent of shrub cover)	
	Backslope (includes footslope and toeslope)	Kinnikinnick (percent of shrub cover)	
	Valley bottom	Fringed sagebrush (percent of shrub cover)	
Stand structure	Closed canopy multistory	Big sagebrush (percent of shrub cover)	
	Closed canopy multistory with open individuals	Bog birch (percent of shrub cover)	
	and/or open scattered clumps	Mountain mahogany (percent of shrub cover)	
	Closed canopy single story with open individuals	Service berry (percent of shrub cover)	
	and/or open scattered clumps	Shrubby cinquefoil (percent of shrub cover)	
	Open canopy, scattered individuals	Bitterbrush (percent of shrub cover)	
	and/or scattered clumps	Skunkbush (percent of shrub cover)	
Disturbance history	Site preparation (tillage)	Rabbitbrush (percent of shrub cover)	
	Artificial regeneration	False rasberry (percent of shrub cover)	
	Natural regeneration (after disturbance)	Wild red rasberry (percent of shrub cover)	
	Stand improvement	Rose (percent of shrub cover)	
	Tree cutting	*Ribes cereum* (percent of shrub cover)	
	Fire	*Ribes inerme* (percent of shrub cover)	
	Other silvicultural treatments	*Vaccinium* spp. (percent of shrub cover)	
	Other human disturbance	Dogwood (percent of shrub cover)	
	Natural disturbance	Snowberry (percent of shrub cover)	
	Land clearing		
	Animal damage		
	Type conversion		
	Mining		
	Grazing		
Total	29	27	3

Table 2.13: Seedling and stand (tree) variables used in statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

Seedling variables	**Stand (tree) variables**
Limber pine seedling height (cm)	Presence of beetles in limber pine
Average terminal growth (mm) of the previous 2 years	Presence of dwarf mistletoe in limber pine
sqrt proportion of limber pine seedlings with wpbr	Presence of wpbr in limber pine
$\log_{10}$ stems/ha of limber pine seedlings	Percent limber pine with bark beetles
$\log_{10}$ stems/ha of all other seedlings	Percent limber pine with dwarf mistletoe
$\log_{10}$ stems/ha of other pine seedlings	Percent limber pine with wpbr
$\log_{10}$ stems/ha of aspen seedlings	Proportion of limber pine with dbh < 5 cm
$\log_{10}$ stems/ha of spruce-fir seedlings	Proportion of limber pine with dbh > 5 - 10 cm
$\log_{10}$ stems/ha of all seedlings	Proportion of limber pine with dbh > 10 - 20 cm
Limber pine seedling presence on a subplot	Proportion of limber pine with dbh >20 cm
Presence of wpbr on a limber pine seedling	Proportion of limber pine in the codominant (includes dominant) crown class
Presence of dwarf mistletoe on a limber pine seedling	Proportion of limber pine in the intermediate crown class
Dead top on limber pine seedlings	Proportion of limber pine in the open-grown crown class
Forbs as dominant groundcover next to seedling	Proportion of limber pine in the overtopped
Grass as dominant groundcover next to seedling	Crown dieback (percent)
Lichens/moss as dominant groundcover next to seedling	$\log_{10}$ stems/ha of limber pine
Litter as dominant groundcover next to seedling	$\log_{10}$ basal area (m²/ha) of limber pines
Rock as dominant groundcover next to seedling	$\log_{10}$ basal area (m²/ha) of limber pines with bark beetles
Shrubs as dominant groundcover next to seedling	$\log_{10}$ basal area (m²/ha) of limber pines with dwarf mistletoe
Soil as dominant groundcover next to seedling	$\log_{10}$ basal area (m²/ha) of limber pines with wpbr
Tree/log as dominant groundcover next to seedling	$\log_{10}$ basal area (m²/ha) of limber pines with bark beetles and dwarf mistletoe
Log as a seedling microsite object	$\log_{10}$ stems/ha of other pines
Rock as a seedling microsite object	$\log_{10}$ basal area (m²/ha) of other pines
Shrub as seedling microsite object	$\log_{10}$ basal area (m²/ha) of other pines with bark beetles
Stump as a seedling microsite object	$\log_{10}$ basal area (m²/ha) of other pines with dwarf mistletoe
Tree/log as a seedling microsite object	$\log_{10}$ stems/ha of all pines
	$\log_{10}$ basal area (m²/ha) of all pines
	$\log_{10}$ basal area (m²/ha) of all pines with bark beetles
	$\log_{10}$ basal area (m²/ha) of all pines with dwarf mistletoe
	$\log_{10}$ stems/ha of all other species
	$\log_{10}$ basal area (m²/ha) of all other species
	$\log_{10}$ stems/ha all live trees
	$\log_{10}$ basal area (m²/ha) all live trees
	$\log_{10}$ dbh of all live trees
	$\log_{10}$ stems/ha of aspen
	$\log_{10}$ basal area (m²/ha) of aspen
	$\log_{10}$ stems/ha of spruce-fir
	$\log_{10}$ basal area (m²/ha) of spruce-fir
	$\log_{10}$ stems/ha of spruce-fir
	$\log_{10}$ tree cankers/ha
	proportion of basal area (m²/ha) of limber pine trees
	$\log_{10}$ stems/ha all trees
	$\log_{10}$ basal area (m²/ha) all trees
	$\log_{10}$ stems/ha all dead trees
	$\log_{10}$ basal area (m²/ha) all dead trees
	$\log_{10}$ dbh of all dead trees
Total: 26	Total: 46

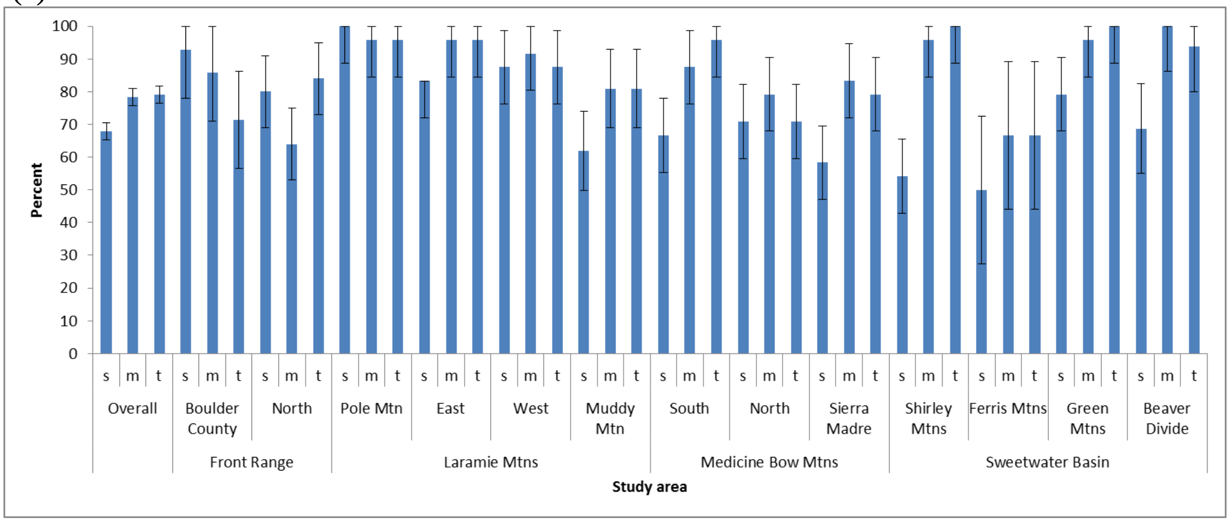
Table 2.14: Meteorological variables obtained from the PRISM dataset (Daly et al. 2002) provided by FHTET (USDA FS Forest Health Technology Enterprise Team, Fort Collins, CO) used in statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

240 m data		30 m data
12 month moderate or greater drought frequency	Average minimum temperature in July - September	Growing season precipitation (mm)
36 month moderate or greater drought frequency	Average maximum temperature in the warmest month	Annual precipitation (mm)
60 month moderate or greater drought frequency	Average maximum temperature for year	Mean annual temperature - tenths of degrees C
Autumn frost date	Average maximum temperature in January	Maximum temperature in the warmest month - tenths of degrees C
Spring frost day	Average maximum temperature in February	Minimum temperature in the coldest month - tenths of degrees C
Frost free period	Average maximum temperature in March	Average temperature in the coldest month - tenths of degrees C
Growing degree days	Average maximum temperature in April	Average temperature in the warmest month - tenths of degrees C
Three-year (2006 - 2008) standardized moisture difference z-score	Average maximum temperature in May	1st principle component monthly precipitation
Three-year (2007 - 2009) standardized moisture difference z-score	Average maximum temperature in June	2nd principle compoent monthly precipitation
Five-year (2004 - 2008) standardized moisture difference z-score	Average maximum temperature in July	Ratio of growing season precip to annual precip - No units (index)
Five-year (2005 - 2009) standardized moisture difference z-score	Average maximum temperature in August	Seasonal moisture index, the ratio of degree-days >5 °C
growing season precipitation (mm)	Average maximum temperature in September	accumulating within the frost-free period to seasonal precipitation
Annual moisture index: the ratio of degree-days > 5 degrees	Average maximum temperature in October	Direct short-wave radiation
celsius to annual precipitation in millimeters.	Average maximum temperature in November	Diffuse short-wave radiation
Mean annual ppt	Average maximum temperature in December	Derived short-wave radiation
Mean January precipitation (mm)	Average maximum temperature in May - June	Short-wave radiation
Mean February precipitation (mm)	Average maximum temperature in July - September	1st principle component average temperature
Mean March precipitation (mm)	Average temperature in the warmest month	1st principle component maximum temperature
Mean April precipitation (mm)	Average temperature for year (mean annual temp)	1st principle component minimum temperature
Mean May precipitation (mm)	Average temperature in January	2nd principle compoent minimum temperature
Mean June precipitation (mm)	Average temperature in February	Water vapor pressure
Mean July precipitation (mm)	Average temperature in March	Soil component dominance
Mean August precipitation (mm)	Average temperature in April	Soil component frequency
Mean September precipitation (mm)	Average temperature in May	Julian date when the sum of degree-days >5 °C reaches 100 - Date
Mean October precipitation (mm)	Average temperature in June	Degree-days <0 °C - degree days
Mean November precipitation (mm)	Average temperature in July	Degree-days >5 °C - degree days
Mean December precipitation (mm)	Average temperature in August	Soil drainage index - derived from SSURGO/STATSGO/NFS
Mean May - June precipitation (mm)	Average temperature in September	Soil data source - SSURGO/STATSGO/USFS
Mean July - September precipitation (mm)	Average temperature in October	Frost-free days - # Days
Ratio GS ppt : Mean annual ppt	Average temperature in November	Julian date of the first freezing date of autumn - Date
Seasonal moisture index, the ratio of degree-days >5 °C	Average temperature in December	Length of the frost-free period - # Days
accumulating within the frost-free period to seasonal precipitation	Average temperature in May - June	Fertility index - derived from SSURGO/STATSGO/NFS
Short wave radiation	Average temperature in July - September	Growing-degree days
Average temperature in the coldest month	Water vapor pressure	Degree-days >5 °C accumulating within the frost-free period
Average minimum temperature in the coldest month	Annual average relative humidity	Julian date of the last freezing date of spring - Date
Average minimum temperature in January	Average relative humidity in January	Topographic Relative Moisture Index
Average minimum temperature in February	Average relative humidity in February	Topographic Relative Moisture Index - Modified
Average minimum temperature in March	Average relative humidity in March	Topographic scale
Average minimum temperature in April	Average relative humidity in April	
Average minimum temperature in May	Average relative humidity in May	
Average minimum temperature in June	Average relative humidity in June	
Average minimum temperature in July	Average relative humidity in July	
Average minimum temperature in August	Average relative humidity in August	
Average minimum temperature in September	Average relative humidity in September	
Average minimum temperature in October	Average relative humidity in October	
Average minimum temperature in November	Average relative humidity in November	
Average minimum temperature in December	Average relative humidity in December	
Average minimum temperature in May - June	Average relative humidity in May - June	
	Average relative humidity in July - September	
	Total: 133	

Table 2.15: Meteorological variables extracted from Daymet Daily Surface Gridded Data used in statistical modeling from a monitoring study of limber pine stands in Colorado, Wyoming, and Montana in 2011 and 2012.

Total precipitation (mm) 2007-2010	Average relative humdity in January 2007	Total precipitation (mm) in January 2007	Maximum temperature in January 2007	Minimum temperature in January 2007
May precipitation (mm) 2007-2010	Average relative humdity in February 2007	Total precipitation (mm) in February 2007	Maximum temperature in February 2007	Minimum temperature in February 2007
May-June precipitation (mm) 2007-2010	Average relative humdity in March 2007	Total precipitation (mm) in March 2007	Maximum temperature in March 2007	Minimum temperature in March 2007
July-September precipitation (mm) 2007-2010	Average relative humdity in April 2007	Total precipitation (mm) in April 2007	Maximum temperature in April 2007	Minimum temperature in April 2007
Average relative humidty 2007-2010	Average relative humdity in May 2007	Total precipitation (mm) in May 2007	Maximum temperature in May 2007	Minimum temperature in May 2007
May relative humidty 2007-2010	Average relative humdity in June 2007	Total precipitation (mm) in June 2007	Maximum temperature in June 2007	Minimum temperature in June 2007
May-June relative humidity 2007-2010	Average relative humdity in July 2007	Total precipitation (mm) in July 2007	Maximum temperature in July 2007	Minimum temperature in July 2007
July-September relative humidty 2007-2010	Average relative humdity in August 2007	Total precipitation (mm) in August 2007	Maximum temperature in August 2007	Minimum temperature in August 2007
Average maximum temperature 2007-2010	Average relative humdity in September 2007	Total precipitation (mm) in September 2007	Maximum temperature in September 2007	Minimum temperature in September 2007
May maximum temperature 2007-2010	Average relative humdity in October 2007	Total precipitation (mm) in October 2007	Maximum temperature in October 2007	Minimum temperature in October 2007
May-June maximum temperature 2007-2010	Average relative humdity in November 2007	Total precipitation (mm) in November 2007	Maximum temperature in November 2007	Minimum temperature in November 2007
July-September maximum temperature 2007-2010	Average relative humdity in December 2007	Total precipitation (mm) in December 2007	Maximum temperature in December 2007	Minimum temperature in December 2007
Average minimum temperature 2007-2010	Average relative humdity in January 2008	Total precipitation (mm) in January 2008	Maximum temperature in January 2008	Minimum temperature in January 2008
May minimum temperature 2007-2010	Average relative humdity in February 2008	Total precipitation (mm) in February 2008	Maximum temperature in February 2008	Minimum temperature in February 2008
May-June minimum temperature 2007-2010	Average relative humdity in March 2008	Total precipitation (mm) in March 2008	Maximum temperature in March 2008	Minimum temperature in March 2008
July-September minimum temperature 2007-2010	Average relative humdity in April 2008	Total precipitation (mm) in April 2008	Maximum temperature in April 2008	Minimum temperature in April 2008
Total precipitation (mm) 2010-2011	Average relative humdity in May 2008	Total precipitation (mm) in May 2008	Maximum temperature in May 2008	Minimum temperature in May 2008
Total precipitation (mm) 2009-2010	Average relative humdity in June 2008	Total precipitation (mm) in June 2008	Maximum temperature in June 2008	Minimum temperature in June 2008
May-September total precipitation 2010-2011	Average relative humdity in July 2008	Total precipitation (mm) in July 2008	Maximum temperature in July 2008	Minimum temperature in July 2008
May-September total precipitation 2009-2010	Average relative humdity in August 2008	Total precipitation (mm) in August 2008	Maximum temperature in August 2008	Minimum temperature in August 2008
October-April total precipitation 2010-2011	Average relative humdity in September 2008	Total precipitation (mm) in September 2008	Maximum temperature in September 2008	Minimum temperature in September 2008
October-April total precipitation 2009-2010	Average relative humdity in October 2008	Total precipitation (mm) in October 2008	Maximum temperature in October 2008	Minimum temperature in October 2008
May-September maximum temperature 2010-2011	Average relative humdity in November 2008	Total precipitation (mm) in November 2008	Maximum temperature in November 2008	Minimum temperature in November 2008
May-September maximum temperature 2009-2010	Average relative humdity in December 2008	Total precipitation (mm) in December 2008	Maximum temperature in December 2008	Minimum temperature in December 2008
May-June maximum temperature 2010-2011	Average relative humdity in January 2009	Total precipitation (mm) in January 2009	Maximum temperature in January 2009	Minimum temperature in January 2009
May-June maximum temperature 2009-2010	Average relative humdity in February 2009	Total precipitation (mm) in February 2009	Maximum temperature in February 2009	Minimum temperature in February 2009
July-September maximum temperature 2010-2011	Average relative humdity in March 2009	Total precipitation (mm) in March 2009	Maximum temperature in March 2009	Minimum temperature in March 2009
July-September maximum temperature 2009-2010	Average relative humdity in April 2009	Total precipitation (mm) in April 2009	Maximum temperature in April 2009	Minimum temperature in April 2009
May-September minimum temperature 2010-2011	Average relative humdity in May 2009	Total precipitation (mm) in May 2009	Maximum temperature in May 2009	Minimum temperature in May 2009
May-September minimum temperature 2009-2010	Average relative humdity in June 2009	Total precipitation (mm) in June 2009	Maximum temperature in June 2009	Minimum temperature in June 2009
May-June minimum temperature 2010-2011	Average relative humdity in July 2009	Total precipitation (mm) in July 2009	Maximum temperature in July 2009	Minimum temperature in July 2009
May-June minimum temperature 2009-2010	Average relative humdity in August 2009	Total precipitation (mm) in August 2009	Maximum temperature in August 2009	Minimum temperature in August 2009
July-September minimum temperature 2010-2011	Average relative humdity in September 2009	Total precipitation (mm) in September 2009	Maximum temperature in September 2009	Minimum temperature in September 2009
July-September minimum temperature 2009-2010	Average relative humdity in October 2009	Total precipitation (mm) in October 2009	Maximum temperature in October 2009	Minimum temperature in October 2009
Average relative humidity in 2000	Average relative humdity in November 2009	Total precipitation (mm) in November 2009	Maximum temperature in November 2009	Minimum temperature in November 2009
Average relative humidity in 2001	Average relative humdity in December 2009	Total precipitation (mm) in December 2009	Maximum temperature in December 2009	Minimum temperature in December 2009
Average relative humidity in 2002	Average relative humdity in January 2010	Total precipitation (mm) in January 2010	Maximum temperature in January 2010	Minimum temperature in January 2010
Average relative humidity in 2003	Average relative humdity in February 2010	Total precipitation (mm) in February 2010	Maximum temperature in February 2010	Minimum temperature in February 2010
Average relative humidity in 2004	Average relative humdity in March 2010	Total precipitation (mm) in March 2010	Maximum temperature in March 2010	Minimum temperature in March 2010
Average relative humidity in 2005	Average relative humdity in April 2010	Total precipitation (mm) in April 2010	Maximum temperature in April 2010	Minimum temperature in April 2010
Average relative humidity in 2006	Average relative humdity in May 2010	Total precipitation (mm) in May 2010	Maximum temperature in May 2010	Minimum temperature in May 2010
Average relative humidity in 2007	Average relative humdity in June 2010	Total precipitation (mm) in June 2010	Maximum temperature in June 2010	Minimum temperature in June 2010
Average relative humidity in 2008	Average relative humdity in July 2010	Total precipitation (mm) in July 2010	Maximum temperature in July 2010	Minimum temperature in July 2010
Average relative humidity in 2009	Average relative humdity in August 2010	Total precipitation (mm) in August 2010	Maximum temperature in August 2010	Minimum temperature in August 2010
Average relative humidity in 2010	Average relative humdity in September 2010	Total precipitation (mm) in September 2010	Maximum temperature in September 2010	Minimum temperature in September 2010
Total precipitation (mm) in 2000	Average relative humdity in October 2010	Total precipitation (mm) in October 2010	Maximum temperature in October 2010	Minimum temperature in October 2010
Total precipitation (mm) in 2001	Average relative humdity in November 2010	Total precipitation (mm) in November 2010	Maximum temperature in November 2010	Minimum temperature in November 2010
Total precipitation (mm) in 2002	Average relative humdity in December 2010	Total precipitation (mm) in December 2010	Maximum temperature in December 2010	Minimum temperature in December 2010
Total precipitation (mm) in 2003	Maximum temperature in 2000	Minumum temperature in 2000		
Total precipitation (mm) in 2004	Maximum temperature in 2001	Minumum temperature in 2001		
Total precipitation (mm) in 2005	Maximum temperature in 2002	Minumum temperature in 2002		
Total precipitation (mm) in 2006	Maximum temperature in 2003	Minumum temperature in 2003		
Total precipitation (mm) in 2007	Maximum temperature in 2004	Minumum temperature in 2004		
Total precipitation (mm) in 2008	Maximum temperature in 2005	Minumum temperature in 2005		
Total precipitation (mm) in 2009	Maximum temperature in 2006	Minumum temperature in 2006		
Total precipitation (mm) in 2010	Maximum temperature in 2007	Minumum temperature in 2007		
	Maximum temperature in 2008	Minumum temperature in 2008		
	Maximum temperature in 2009	Minumum temperature in 2009		
	Maximum temperature in 2010	Minumum temperature in 2010		
		Total: 270		

(a)



b)

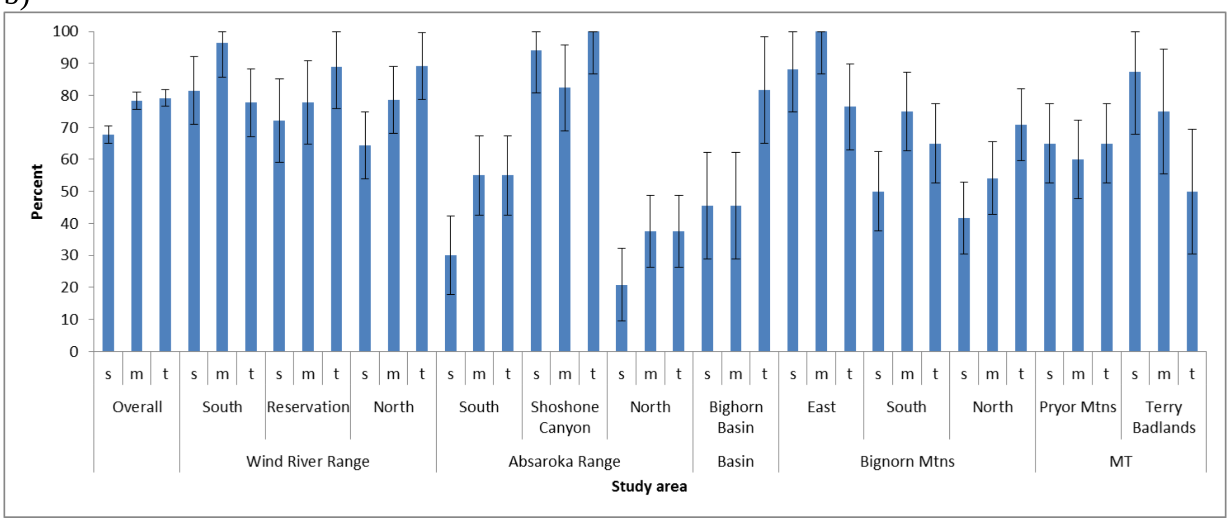


Figure 2.7: Occurrence (least square means using PROC GLIMMIX) of live limber pine seedlings on a plot in three height classes (s: small 0-45.7 cm, m: medium >45.7-91.4 cm, and t: tall >91.4-137 cm) in the (a) southern Rocky Mountains and (b) central Rocky Mountains from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Values are adjusted for study area and height category. Error bars are ± half approximate LSD.

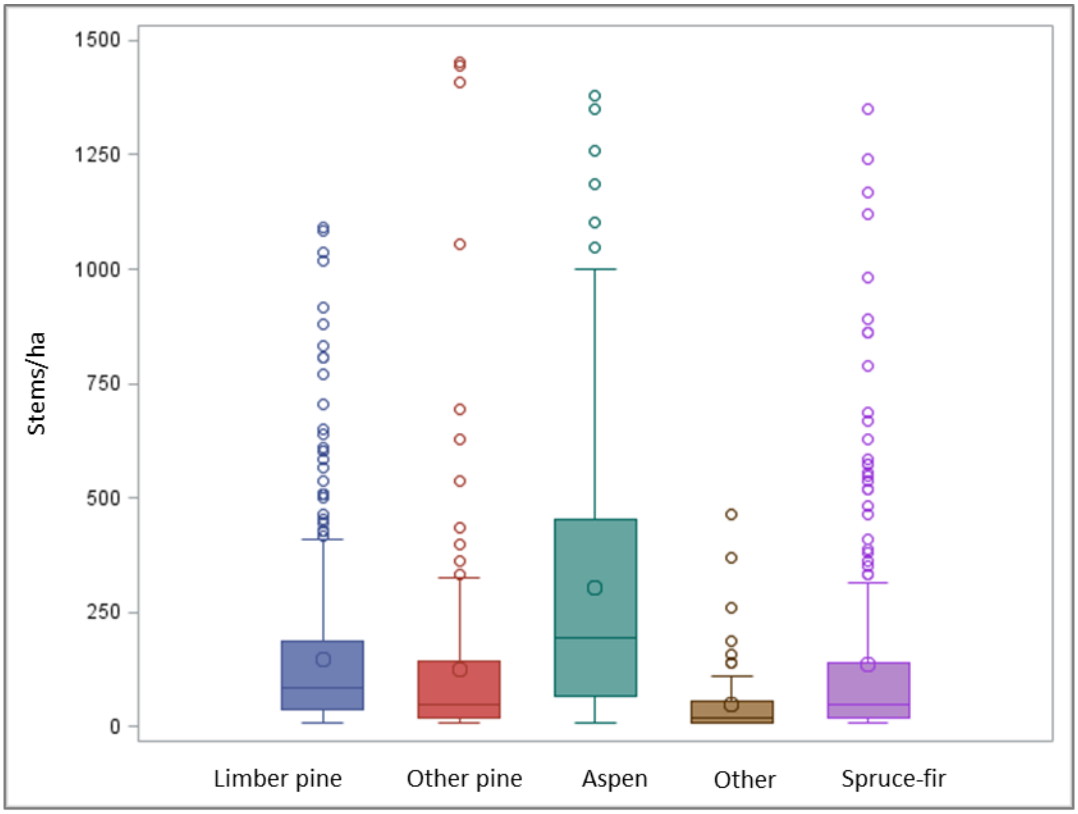


Figure 2.8: Density (stems/ha) of live seedlings in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012.

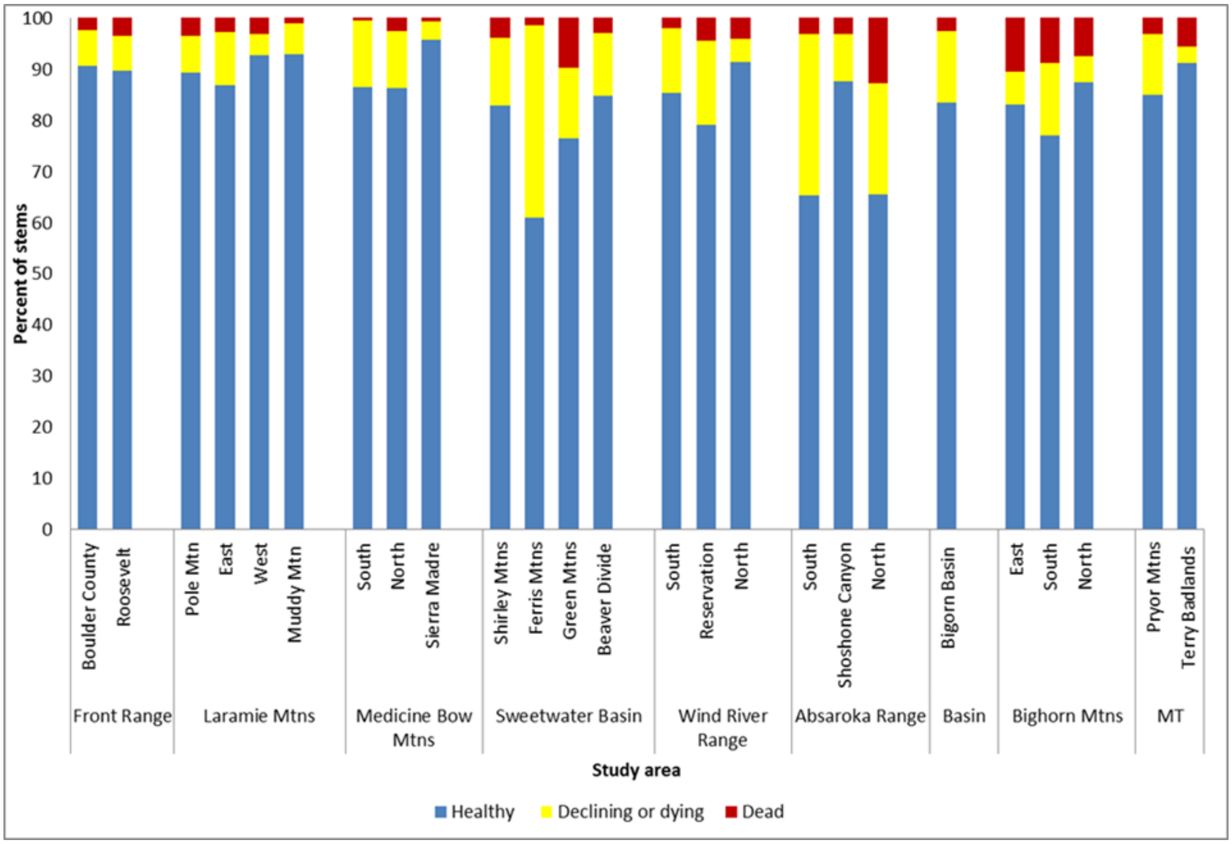


Figure 2.9: Health status of limber pine seedlings in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Healthy = no visual damage to crown or stem up to 5% damage, declining/dying = 6-50% of crown showing symptoms that indicates it is dead or will be or >50% of crown showing symptoms or is damaged, dead = recent dead (no green needles, red needles but fines still present), old dead (no fine twigs, no needles, >50% bark still present), very old dead (no fine twigs, no needles, <50% of bark present).

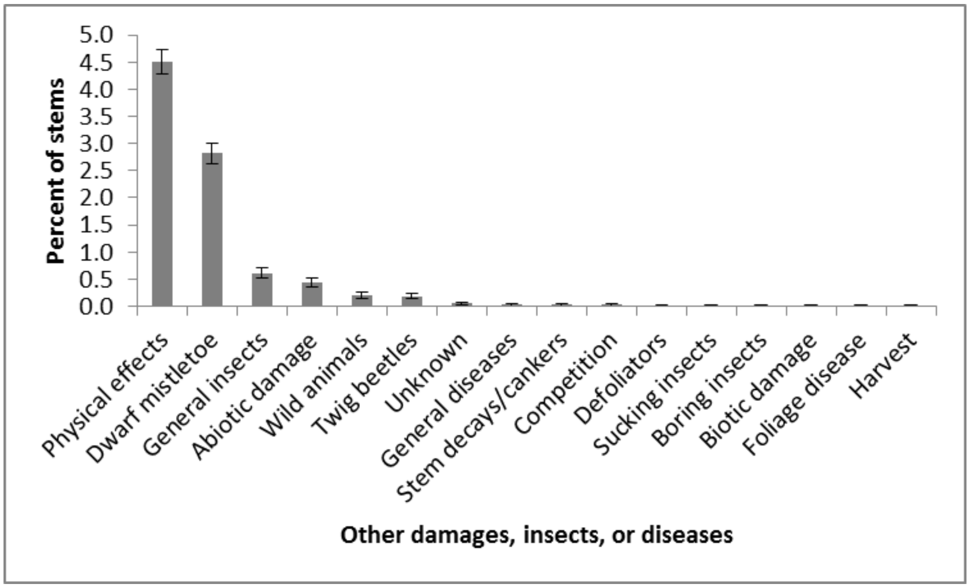
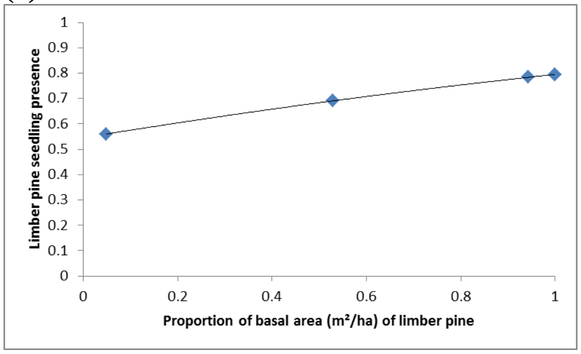


Figure 2.10: Other damage agents (insect, abiotic, and biotic) that occurred on limber pine seedlings.

(a)



(b)

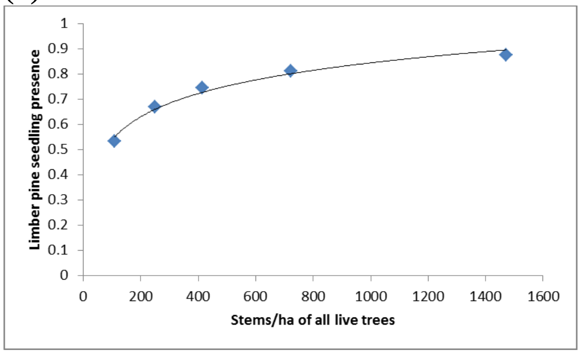
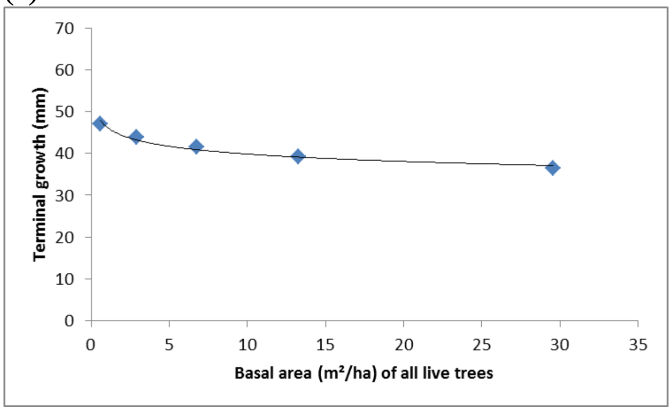
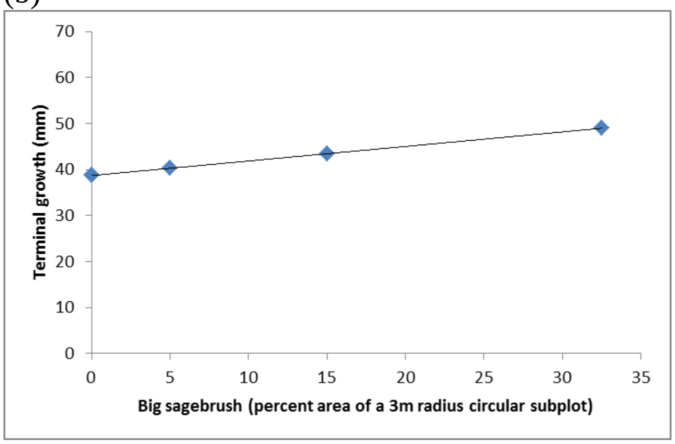


Figure 2.11: Logistic regression analysis predicting limber pine seedling presence on a subplot using variables selected in the final model (fit using PROC GLIMMIX with study area as a random effect, in SAS) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Relationship with response variable was plotted using mean values and the 5th, 25th, 50th, 75th, and 95th percentiles. Predicted values were back transformed. Positive relationships exist between (a) limber pine seedling presence on a subplot and proportion of basal area (m²/ha) of limber pine trees and (b) stems/ha of all live trees.

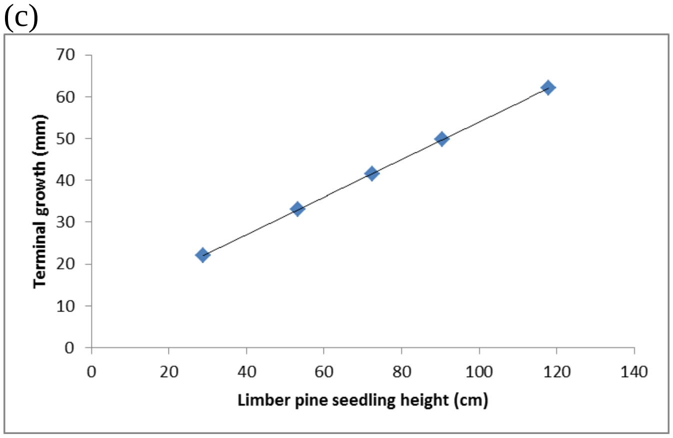
(a)


70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
35
Terminal growth (mm)
Basal area (m²/ha) of all live trees

(b)


70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
35
Terminal growth (mm)
Big sagebrush (percent area of a 3m radius circular subplot)

(c)


70
60
50
40
30
20
10
0
0
20
40
60
80
100
120
140
Terminal growth (mm)
Limber pine seedling height (cm)

(d)

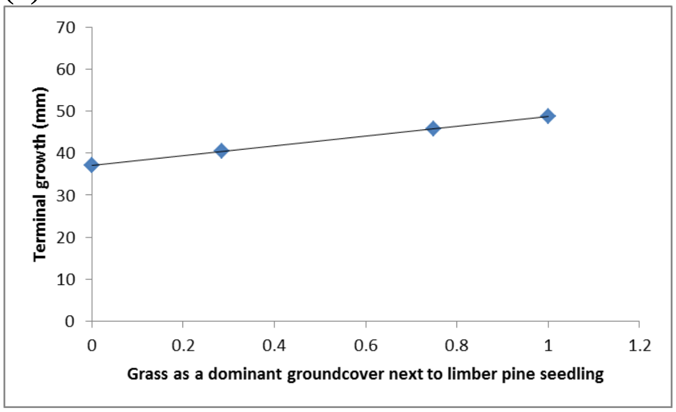
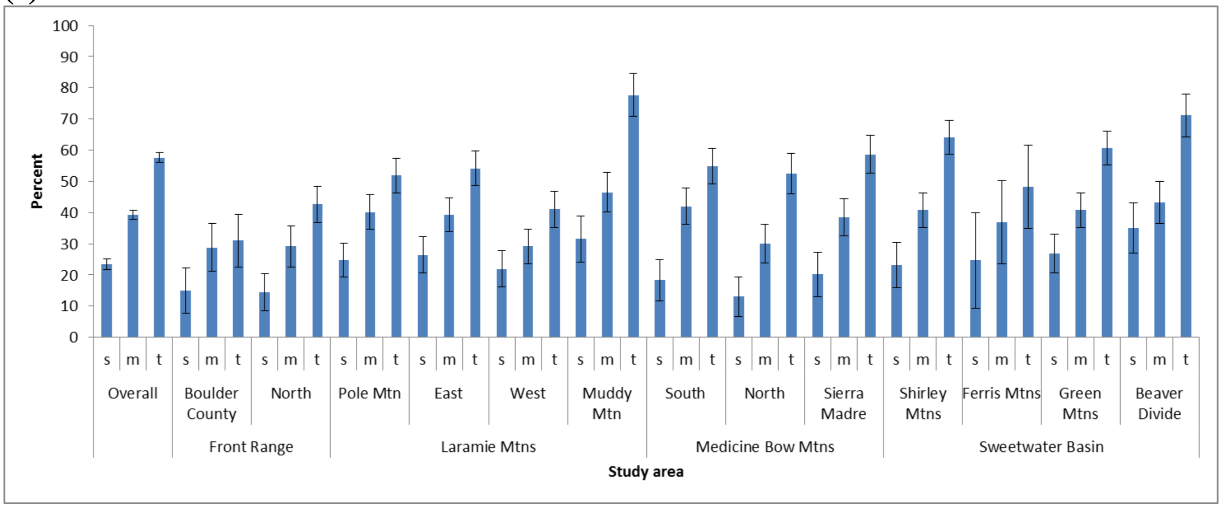


Figure 2.12: Linear regression analysis predicting limber pine seedling terminal growth (mm) on a subplot using variables selected in the final model (fit using PROC MIXED with study area as a random effect, in SAS) from a monitoring study of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Relationship with response variable was plotted using mean values and the 5th, 25th, 50th, 75th, and 95th percentiles. Predicted values were back transformed. A negative relationship exists between (a) limber pine seedling terminal growth (mm) on a subplot and basal area (m^2/ha) of all live trees. Positive relationships exist between (b) limber pine terminal growth (mm) on a subplot and big sagebrush (percent of a 3m radius circular subplot), (c) limber pine seedling height (cm), and (d) grass.

(a)



(b)

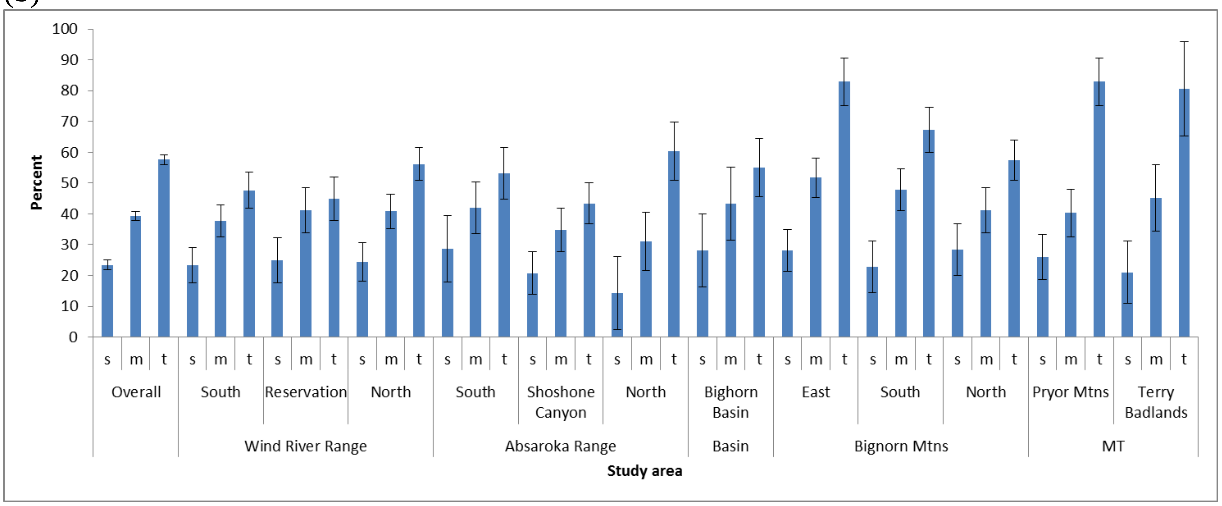


Figure 2.13: Average terminal growth (mm) (least square means) of the previous two years (from year of measurement) of limber pine seedling growth in three height classes (s: small 0-45.7 cm, m: medium 45.7-91.4 cm, and t: tall 91.4-137 cm) in the (a) southern Rocky Mountains and (b) central Rocky Mountains from a survey of limber pine stands in 25 study areas in Colorado, Wyoming, and Montana in 2011 and 2012. Values are adjusted for study area and height category?. Error bars are ± half approximate LSD.

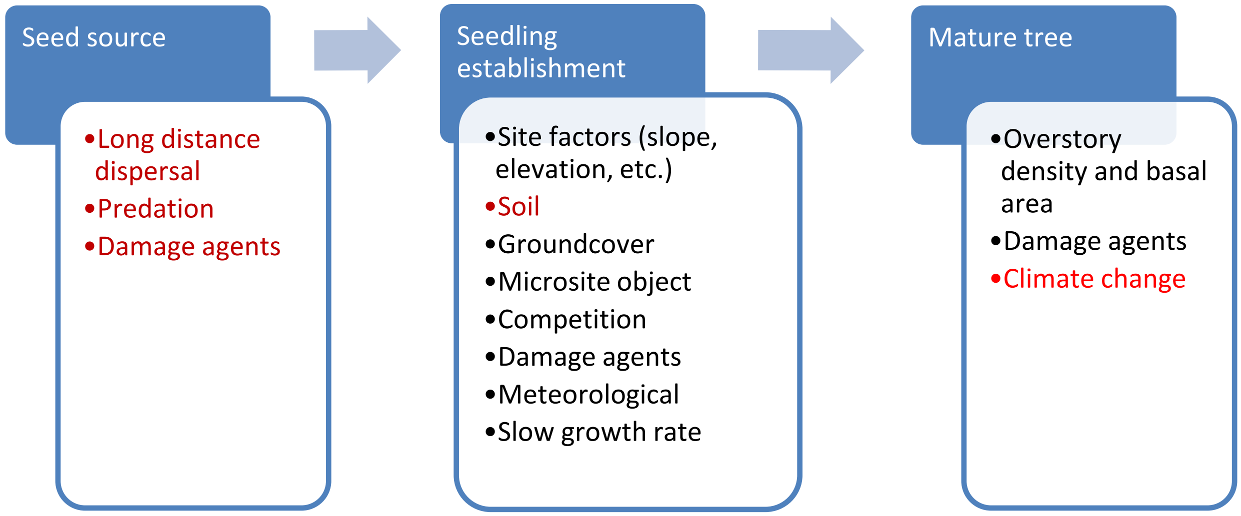


Figure 2.14: Factors that potentially affect limber pine regeneration. Factors in red were not addressed in this study.

Appendix III: Additional Regeneration Information and References

Regeneration from nutcracker caches may occur in clusters (Woodmansee 1977) since seeds are often cached in groups of up to 15 seeds (Tomback 1982). In the front range of Colorado, about 20 percent of tree sites, including higher elevations, tend to be clustered but can range wildly by site (5-77%) (Carsey and Tomback 1994). The clustered growth pattern aids in survivorship of limber pines on harsh sites but may be unfavorable on mesic sites with spruce-fir (Donnegan and Rebertus 1999). Clark's nutcracker tends to cache seeds in lower-elevation forested areas relative to home range (Lorenz et al. 2011) but may cache seeds in microsites at high elevations, above ground (i.e. in trees) (Lorenz et al. 2011), in burn areas (Lanner and Vander Wall 1980), or windswept sites that lack snow accumulation (Vander Wall and Balda 1977). Limber pine can regenerate on sites post-disturbance (fire) where it was once established, particularly if site conditions favor establishment (xeric, windswept), but if seed dispersal by Clark's nutcracker is limited, some of these sites may not regenerate (Shankman and Daly 1988).

References

Carsey, K.S. and Tomback, D.F. 1994. Growth form distribution and genetic relationships in tree clusters of *Pinus flexilis*, a bird-dispersed pine. Oecologia 98:402-411.

Vander Wall, S.B. and Balda, R.P. 1977. Coadaptations of the Clark's Nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecological Monographs 47:89-111.

Woodmansee, R.G. 1977. Clusters of limber pine trees: a hypothesis of plant-animal coaction. The Southwest Naturalist 21(4):511-517.