THESIS

TIME SERIES ANALYSIS OF LIMBER PINE (*PINUS FLEXILIS)* HEALTH IN THE U.S. ROCKY MOUNTAINS IN RESPONSE TO WHITE PINE BLISTER RUST (*CRONARTIUM RIBICOLA*) AND BARK BEETLES

Submitted by

K. A. Leddy

Graduate Degree Program in Cell and Molecular Biology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2018

Master's Committee:

Advisor: Jane E. Stewart

Zaid Abdo
Dan Sloan
Anna Schoettle
Howard Liber

ABSTRACT

TIME SERIES ANALYSIS OF LIMBER PINE (PINUS FLEXILIS) HEALTH IN THE U.S. ROCKY MOUNTAINS IN RESPONSE TO WHITE PINE BLISTER RUST (CRONARTIUM RIBICOLA) AND BARK BEETLES

From 2004-2007, 106 permanent limber pine monitoring plots were established and measured throughout the U.S. Rocky Mountains (MT, WY, CO) to characterize health trends in response to white pine blister rust (WPBR) and bark beetles (including mountain pine beetle, “MPB”, and *Ips* spp., “Ips”) over time. These plots were subsequently measured in 2011-2013 and again in 2016-17 to form a time series analysis of limber pine health. Data were gathered on 8,206 monumented trees (4,176 limber pine) and included measurements on various stand, ground cover, and landscape characteristics over the three time intervals.

The overall percentage of live trees infected with WPBR was 29.4% in 2004-07 and 25.7% in 2016-17, with incidence decreasing in parts of Wyoming (Pole Mountain, Laramie Peak), increasing in southern Colorado (Sangre de Cristo Mountains), and stable in other subregions. However, of limber pines that were healthy during the first measurement, 22.2% were declining/dying and 21.1% had died by the end of the study period due to WPBR and/or bark beetle damages. Due to this, it is likely that new WPBR infections are occurring as the large number of live, infected trees dying during the survey may have masked newly infected trees in incidence calculations. In heavily WPBR-infected areas such as Pole Mountain, Wyoming, 65% of live trees were infected (in 2004-07), and of trees that began the study as healthy, 23% were declining or dying and 38% had died by the end of the study period (2016-17). Additionally,

WPBR severity increased significantly from the beginning of the study with 4 previously uninfected sites gaining WPBR infections, 29 sites advancing to ‘moderately infected’ and 5 sites becoming ‘heavily infected’. The overall average number of cankers per tree (3.5) was stable, but the number of infected limber pine with a canker in the lower 1/3 of the stem (18%) increased significantly (+4.2%, $P = 0.001$). When examining all limber pine in the study, 8%, 3% and 3% were killed by MPB/Ips., WPBR, and combined effects of these agents, respectively. Of the 887 live, but declining or dying limber pine, 52% had WPBR infections and 38% had damage from twig beetles (*Pityophthorus* spp., *Pityogenes* spp.) in 2016-17. Though all sites had ≥ 20% limber pine composition, 34% of sites had no limber pine regeneration and 7% had no regeneration of any tree species over the entirety of the study period.

The results of this time series indicate that limber pine populations in the U.S. Rocky Mountains are declining due to effects from WPBR and MPB/Ips. Long-term surveys capture the effects of these damage agents on native tree populations and provide critical guidance for future management and restoration of these ecologically valuable species.

Limber pine is at risk due to the various biotic and abiotic agents threatening their health. Thus, future directions involve restorative management practices for highly impacted areas where limber pine is a climax species and proactive management for healthy limber stands to promote resilience to likely damage agents. In highly impacted areas (WPBR incidence, mortality, or bark beetle damage on >50% of trees and low limber pine density and regeneration), where limber pine co-exists with other tree species, it may be favorable to allow the natural succession of other tree species to become dominant. However in xeric, harsh sites where limber pine is a climax species, these highly impacted areas are at-risk for losing all tree cover and should be considered for protective and restorative planting strategies. As natural resistance to WPBR occurs on the landscape, genetic screening and protection of mature limber pine carrying either complete or partial resistance to the pathogen should be pursued to preserve this genetic diversity. A priority should be to protect resistant trees against bark beetles and fire using established management practices. Additionally, seed-sourcing from resistant trees can allow for resistant progeny to be out-planted into high priority areas, thus buffering stands at risk for high WPBR mortality. Moreover management plans that promote diversification of age and diameter classes within stands can provide resilience against pest and pathogen attacks, as bark beetles vary in diameter preference and WPBR infections tend to cause higher mortality in smaller diameter trees. Lastly in healthy limber pine stands, proactive management of pest impacts to promote stand resilience is recommended as in Schoettle & Sniezko (2007) in order to preserve these healthy populations.

ACKNOWLEDGMENTS

I would like to thank the following individuals and agencies for their contribution to this research: A. McMahan, F. Krist and W. Monahan (USDA Forest Health Assessment and Applied Sciences Team, FHAAST); Statistical guidance from Z. Abdo (Microbiology, Immunology, and Pathology Dept., Colorado State University) and P. Turk (Franklin A. Graybill Statistical Laboratory, Colorado State University); F. Bunch (Great Sand Dunes National Park and Preserve); B. Verhulst (Rocky Mountain National Park); P. Bovin (National Park Service); J. Walla (Northern Tree Specialties); USDA Forest Service personnel from the Flathead, Lewis & Clark, Beaverhead-Deerlodge, Gallatin, Black Hills, Bighorn, Shoshone, Medicine Bow-Routt, Arapaho-Roosevelt, and San Isabel National Forests; J. Gilham (Blackfeet Nation); J. Blodgett (USFS Region 2), and M. Jackson (USFS Region 1). A special thank you to the hard working field crew members and data entry personnel: C. Holtz, L. DuCharme, J. Ibarra-Caballero, B. Lalande, R. Sitz, S. Espinosa Miller, B. Stone, A. Chambers, D. Shorrock. Thank you to Kelly Burns, the forestry queen; Anna Schoettle, an inspiration and pinnacle of excellence for female researchers in forestry; and William Jacobi, the forest heath guru; this research wouldn't have been possible without the help of these incredible scientists. I also want to extend a deep gratitude to my graduate committee for their effort and commitment to my progress as a scientist. Lastly a big thank you to my advisor Jane for putting up with me, a monumental task in itself.

DEDICATION

This thesis is dedicated to my incredible mother, for she defines the meaning of 'only a mother's love' and I am continually amazed at the extent of her kindness and caring. Additionally, to my father who has always been there for me in my times of need, thank you.

I would also like to dedicate this writing and the efforts that went into it to my late aunt, Linda, for she was a champion for my uniqueness. I want to thank her for always supporting me, even in my most bizarre ventures, I will never forget how unconditionally she loved and the life lessons she so graciously taught me.

Lastly, I want to thank Elliot, my soulmate, for always sticking by my side even when times are hard. And of course, for being equally as weird as I.

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CHAPTER 1: INTRODUCTION

Since its accidental introduction to western North America in the early 20th century, white pine blister rust (WPBR, caused by *Cronartium ribicola* J.C. Fisch.) has devastated white pine populations within their natural ranges with further impacts imposed by the recent mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) epidemic (Kearns & Jacobi 2007, Cleaver et al. 2015, Cleaver et al. 2017, Jacobi et al. 2019). In the Rocky Mountains, the combined effects of these agents has resulted in rapid population declines of whitebark (*Pinus albicaulis* Engelm.) and limber (*P. flexilis* James) pines and the subsequent elevation of their status to endangered in Canada (Smith et al. 2008, Smith et al. 2013, Species at Risk Act 2002, Wildlife Act 2000).

Limber pine is an important species throughout the Rocky Mountains and spans a vast latitudinal (34°-54°N) and elevational (870 – 3,810m) range (Steele 1990, Figure 1). Its seeds provide a vital food resource for wildlife such as corvids, red squirrels, other small rodents, and black and grizzly bears (Schoettle 2004). Additionally, limber pine often defines upper and lower tree line, growing on exposed rocky slopes where other tree species cannot, thus playing an important role in snowpack retention, erosion control, and maintaining cover on harsh sites (Schoettle 2004). As some of the oldest pines in the Rocky Mountains, limber pines are ecologically and culturally valuable. However, they are understudied and at the same time threatened by WPBR, mountain pine beetle, *Ips* beetles, and changing climates (Burns et al. 2011, Larson 2011, Schoettle 2004). Climate models predict that in regions such as Rocky Mountain National Park, limber pine will be forced to higher elevations (Monahan et al. 2013) and the USFS National Insect and Disease Risk Map predicts a 44% reduction in limber pine basal area by 2027 due to combined effects of MPB/Ips, WPBR and dwarf mistletoe (Krist et al. 2014). Thus, knowledge of the current health status of limber pine and how stands are responding to these damage agents will provide critical information to inform management and guide recovery efforts.

By the early 1920's, the WPBR disease front had spread across Oregon, Washington and Idaho to northern Montana where it continued to move south and east into the Rocky Mountains (Pennington 1925, Brown & Graham 1967). As the disease spread and intensified, it threatened American landmarks such as Glacier, Yellowstone, and Grand Teton National Parks (Brown & Graham 1967, Smith et al. 2011, Harris 1999, Bockino and Tinker 2012). By 1978, the disease had spread across Wyoming but incidence rates were highly variable by geographic region (Brown 1978). *Cronartium ribicola* was first found in Colorado near the Wyoming border in 1998 (Johnson and Jacobi 2000) and has since been found in multiple locations in Colorado including the Sangre de Cristo and Wet Mountains of southern Colorado and the northern and southern Front Range Mountains (e.g. Teller, El Paso, Boulder, and Larimer Counties including Pikes Peak and Rocky Mountain National Park) (Blodgett & Sullivan 2004, Burns 2006, Schoettle et al. 2018). The relatively recent movement of the disease into forests of Colorado coupled with the rising mountain pine beetle epidemic, raised questions as to the future health of white pines in high-elevation areas.

Mountain pine beetle is an aggressive, destructive bark beetle native to western North America. Nearly all western pine species are hosts, but lodgepole (*Pinus contorta*), ponderosa (*P. ponderosa*), whitebark (*P. albicaulis),* and limber (*P. flexilis*) pine are the most common hosts in the Rocky Mountains (Furniss 1977, Alfaro et al. 2003, Gibson 2003, Gibson et al. 2008, Brown and Schoettle 2008). The most recent outbreak (1998-2013) particularly affected limber pine, a favored host of MPB (Cerezke 1995, Langor 1989, Man 2010), with mortality increasing in area from 450 to 50,000 ha (1998-2007) and coinciding with severe drought, warm temperatures, and mild winters (Vorster et al. 2017, Taylor et al. 2006, Logan and Powell 2001). In a typical cycle, MPB populations surge, killing many mature trees then decline as the food source is depleted (Kipfmueller et al. 2002, Gibson et al. 2008, Hart et al. 2015). As the MPB epidemic collapsed in northern Colorado and southern Wyoming, populations of *Ips woodi* Thatcher increased, attacking and killing limber pines in the absence of MPB (Witcosky 2017). *Ips* activity continued for several years adding to the total losses of limber pine in this area over the course of the epidemic.

The ability of limber pine to successfully regenerate has been complicated by emerging factors such as WPBR, prolonged population response to natural disturbance (Coop and Schoettle 2009, Schoettle 2004), and climate change. White pine blister rust quickly girdles young trees and cone-bearing branches on mature trees (Schoettle and Sniezko 2007, Schoettle 2004). Mountain pine beetle and Ips beetles can indiscriminately kill WPBR-resistant trees, reducing the favorable gene pool (Schwandt 2006). Furthermore, evidence suggests that climates are becoming less hospitable for white pines (Larson et al. 2011, Rehfeldt et al. 2008, Malone et al. 2018, Millar et al. 2018), further exacerbating the ability for these species to recover. Information on how limber pine populations are affected by and responding to these stressors is necessary to inform management, conservation, and restoration efforts.

Recent studies have surveyed limber pine populations in response to these biotic agents in a single time point (Kearns & Jacobi 2007, Burns et al. 2011, Cleaver et al. 2015, Cleaver et al. 2017) as well as in multiple time points (Smith et al. 2013). In single time-point surveys, incidence and mortality rates show great variability between and even within mountain ranges

(Cleaver et al 2015, Kearns and Jacobi 2007), demonstrating the complexity of forest health trends in the limber pine-WPBR pathosystem. Sites in Wyoming and Colorado first measured by Kearns and Jacobi (2007) in 2002-04 and remeasured by Cleaver et al. (2015) in 2011-12 had an increase in WPBR incidence of 6% and increase in bark beetle mortality of 17%. Smith et al. (2013) surveyed limber pine throughout its range in the Canadian Rocky Mountains over 6 years from 2003-2009, with some sites surveyed over a 13 year period (1996-2009). Results from this long-term survey demonstrated continued spread of the disease throughout Canada's limber pine range and found 10% increases in infections among live limber pine. Further, Smith et al. (2013) found that limber pine sites at the southernmost edge of their study area, near the U.S. border, showed the highest WPBR infection and mortality rates compared to stands further north. Their study suggested that the long-term persistence of limber pine in these study sites is in jeopardy.

Long-term surveys of permanent plots can provide valuable insights into disease development. This is especially important in forested ecosystems, as changes to tree health may span many years. This time series analysis assessed permanent plots throughout the U.S. Rocky Mountains for 9-13 years in order to measure changes in health status and stand dynamics in limber pine populations impacted by bark beetles and WPBR. The MPB epidemic occurred in the middle of the survey period, thus providing invaluable information on WPBR impacts before and after the outbreak. Aerial surveys provide information on bark beetle trends in limber pine stands, however they cannot give precise estimates of mortality. Our study provides trends in overall limber pine health, mortality from MPB/Ips, incidence/mortality from WPBR, and correlations with 30 years of climate data in the U.S. Rocky Mountains. Results of this long-term study provide insight into temporal trends of the biotic agents threatening the ecologically important limber pine in order to inform landscape monitoring and management plans. The objectives of this study were to i) assess long-term ecological impacts of WPBR and bark beetles on limber pine populations across the U.S. Rocky Mountains, ii) measure and maintain established limber pine plots for future re-measurement and iii) gather information on changes in the distribution, incidence, and severity of WPBR infections and mortality in order to inform management practices to sustain, protect, and restore impacted stands.

CHAPTER 2: MATERIALS & METHODS

Study areas

A total of 106 plots were established in the 2004-2007 field seasons in the U.S. Rocky Mountains representing 5 study areas for long-term monitoring: i) Southern Colorado (SOCO), ii) Northern Colorado/Southern Wyoming (COWY), iii) Northern Wyoming (NOWY), iv) Montana (MT), and v) North Dakota (ND). Sites were selected based on vegetation layers, limber pine composition > 20% in previous surveys, and suggestions from local land managers. From these areas, site locations were randomized across elevational ranges, aspects, slope positions, WPBR incidence (where available), and stand species compositions. Study areas were divided into subregions based on geography. SOCO contains sites in the Sangre de Cristo Mountains (25 sites); COWY contains sites in the southern Poudre Canyon and Rocky Mountain National Park ("Poudre South")(4 sites), Canyon Lakes area (8 sites), Pole Mountain area (8 sites), Snowy Mountain Range (7 sites), and Laramie Peak area (7 sites); NOWY contains sites in the Bighorn Mountains (12 sites) and Shoshone National Forest (Absaroka Mountains, 17 sites); MT contains sites throughout the state (16 sites); and ND contains sites in the badlands of the southwest portion of the state (2 sites) (Figure 1).

Plot design

Plots were established as a belt transect following methods adapted from the Whitebark Pine Ecosystem Foundation (Tomback et al. 2005). Each plot (200' x 50') was divided into three 67'x 50' sections, except in SOCO where plot dimensions varied to include approximately 30 live white pines > 1.3 m tall; but on average were 200' x 50' (Burns et al. 2011) (Supplemental Figure 2). At the center point of each section, a fixed area circular subplot ($1/100^{th}$ acre, 11.8' radius) was established to quantify ground cover, understory vegetation, and regeneration (stems < 1.3 m tall). Plots were monumented with a labeled rebar stake (or PVC pipe) at the center point of each section and at the plot start and end points. Both rebar and PVC stakes were maintained and/or replaced to sustain the monitoring sites throughout the study period (2004-2017) and beyond. Three sections allowed more accurate assessment of stand density and species composition in relation to the data collected within subplots and also assisted with locating trees.

Survey methods

Site measurements

For all sites, plot data regarding transect bearing (and transect length/width in SOCO plots), aspect, slope, elevation, position on slope, stand structure, and disturbance history were recorded. Additionally, the presence of WPBR alternate hosts *Ribes*, *Castilleja*, and *Pedicularis* spp. and a tally of total, WPBR-infected, WPBR-killed, and dead (other causes) limber pine regeneration (< 1.3 m tall) was recorded for the area encompassed by the plot. In each subplot (1/100th acre) percent ground cover of lichen/moss, rock, bare soil, litter, vegetation (shrubs and forbs), and tree stems/downed logs was estimated as well as the three most common shrub species.

Trees > 1.3 m in height

In all sites, stems that forked below 1.3 m were considered separate trees. All tree species (white pines only in SOCO) > 1.3 m tall in the COWY, NOWY, MT, and ND areas were tagged (except those in Rocky Mountain National Park) and the following information were collected: clump status with other trees (for stems splitting < 1.3 m), species, health status (1. healthy: <15% damage to crown/stem; 2. declining: 16-50% damage to crown/stem; 3. dying: >50% damage to crown/stem; 4. recent dead: no green needles, red needles/fine twigs present; 5. old dead: no fine twigs, no needles), diameter at breast height (dbh), crown class (open grown, dominant, codominant, intermediate, overtopped, or krummholtz), and damage agent with severity for any damage impacting >5% of the tree. In SOCO, a variable radius plot was established at the center point of the beginning, center, and end of each plot to collect data on stand composition including species, diameter class (class 1 = <2"; 2 = 2.1"-6"; 3 = 6.1"-12"; 4 = 12.1"-24"; 5 = >24" dbh), and health status (see above) for all “in” trees. Species composition for sites was assessed by categorizing stems as either limber pine (*P. flexilis*) or falling into one of the following categories: ‘Other Pines’: *Pinus contorta* subsp. *latifolia*, *P. ponderosae, P. albicaulis, P. aristata*, ‘Spruce-Fir’: *Pseudotsuga menziesii, Abies lasiocarpa, A. concolor, Picea engelmannii.*, or ‘Other spp.’: *Juniperus scopulorum*, *Populus tremuloides*. For white pines, additional information was collected including live crown ratio (length of live crown divided by tree height), canopy kill (percent of canopy that is killed not including shade-killed branches), percent of branches with live cones by canopy third, and rust-related measurements (see 2.3.3 WPBR assessments). Trees that grew into the > 1.3 m height group during a sampling period were included as current data, tagged, and the above metrics were recorded. Year of attack for MPB/Ips-killed trees was based on degradation classes of needles and fine branches as described by Klutsch et al. (2009). In the initial measurements, trees classified as “old dead” were not evaluated for damage or cause of death, as many were too degraded to accurately determine this information. As a result, many of the measurements made in the 2004-07 sampling regarding mortality and damage agents are zero or underestimated due to the small sample size of dead trees measured (recent dead only).

White pine blister rust assessments

Disease severity was quantified using the rapid rating system developed by Six & Newcomb (2005) throughout the study following plot establishment. Severity was calculated by dividing the crown and stem into thirds and evaluating each crown third by percent of foliage affected by disease and each bole third by percent of surface area affected by cankers. For each third, a score of 0 was assigned to 0% affected, 1 for <25% affected, 2 for 25-50% infected, and 3 for >50% affected (3). The maximum severity score possible per tree is 18, however scores above 14 are highly unlikely as few trees survive with a score >12 (Six & Newcomb 2005). The 6 total scores per tree are summed for all trees in a site and the mean represents severity for the site. Scores for individual trees and site-level mean ranged from 1-4 (light infection), 5-8 (moderate infection), and 9+ (highly infected). Severity was recorded in the 2011-13 and 2016-17 measurements for all subregions except the Sangre de Cristo Mountains. The number of branch and stem cankers per crown third were tallied and categorized as active (aecia/pycnia present), based on indicators (displays at least 3 of the following 5 indicators**:** roughbark, flagging, gnawing, sap production, and/or swelling) (Hoff 1992, GYWPMWG 2011), or dead/inactive (canker caused by WPBR but is no longer active). Canker lengths were also measured for up to six cankers per crown third. Statistical analyses were conducted using the severity ratings for each plot within a subregion.

Regeneration

In each subplot (1/100th acre) all regenerating tree species < 1.3 m tall were evaluated. Data collected included species; height class (< 25 cm or 25-130 cm); WPBR presence/absence and cause of death (WPBR/not WPBR) for white pine species. Due to low sample sizes, in the 2011-13 measurement and onwards white pine regeneration were tallied by species, WPBR presence/absence, and cause of death (WPBR/not WPBR) throughout the entire plot in addition to the subplots.

Climate data

Climate data were obtained from the USDA Forest Health Assessment and Applied Sciences Team (FHAAST) for each plot centroid from years 1985-2016 (Supplemental Table 1). These data were acquired using the methods outlined in Koch et al. (2010) from PRISM, Daymet, and Tree Atlas data sources using the same variables specified in Cleaver et al. (2015).

Data analyses

Data were organized using Microsoft Excel (2013) and statistical calculations were completed in SAS Studio (3.6). WPBR incidence values were estimated for each plot by calculating the number of live, infected trees out of live limber pine surveyed. WPBR mortality was similarly calculated as the number of limber pine killed by *C. ribicola* out of the total number (live and dead) of limber pine. Incidence and mortality means for subregions and overall were determined using a generalized linear mixed model, PROC GLIMMIX, procedure in GLMM mode with plot location as random effect and year as fixed effect. Stand and meteorological variable means were assessed for significant change ($P < 0.05$) from 2004-07 to 2016-17 using a paired T-test, PROC TTEST option 'paired' on count data (not percentages). Standard error was calculated for the change between two means, pooling variance across samplings within a subregion using PROC UNIVARIATE. Comparison of means between subregions was performed using PROC ANOVA on normal or transformed to normal data with Tukey adjustment for multiple comparisons. Similarly, proportional variables such as count data were assessed for significance using McNemar's test for paired proportions, PROC FREQ option 'agree' with exact = 'MCNEM' (McNemar 1947). For correlations between WPBR incidence or mortality and stand/meteorological variables, data were transformed where non-normal and assessed for linearity via scatterplots. Variables with a linear relationship and no outliers were assessed via Pearson correlations whereas nonlinear relationships were assessed via Spearman correlations to capture the strength of association using the PROC CORR procedure option 'Pearson' or 'Spearman', respectively (Supplemental Tables 2-4).

CHAPTER 3: RESULTS

Site characteristics

Permanent plots, ca. 106, were installed during the 2004 (SOCO), 2006 (COWY), and 2007 (NOWY, MT, ND) field seasons. Sites were distributed across aspects: N (10.1% of sites), NE (2.8%), E (12.8%), SE (6.4%), S (16.5%), SW (19.3%), W (15.6%), and NW (15.6%) and slope positions: summit (13.8%), shoulder (28.4%), backslope (33.0%), frontslope (16.5%), and valley bottom (8.3%). Sites were located between 884 – 3119 m (2,900'-10,243') elevation, had an average slope of 25° (Table 1), and contained 8,206 standing trees, 4,176 of which were limber pine (50.9%). Additionally, 57 plots (53.7%) had *Ribes* spp. at the beginning of the study and 14 plots gained *Ribes* spp. resulting in 71 plots (66.9%) with *Ribes* spp. in 2016-17.

Stand characteristics

The average number of live trees per plot (all species) significantly declined from 74 ± 1 in 2004-07 to 69 ± 1 in 2016-17 ($P = 0.01$). Similarly, the average number of live limber pine per plot also declined from 37 ± 1 to 31 ± 1 ($P < 0.05$). Other co-occurring trees included (% of sites in 2004-07 / 2016-17) *Pseudotsuga menziesii* (43.1% / 45.9%), *Populus tremuloides* (33.9% / 45.7%), *Pinus ponderosae* (27.5% / 30.3%), *Pinus contorta* subsp. *latifolia* (23.9% / 23.9%), *Picea engelmannii* (22.0% / 20.2%), *Juniperus scopulorum* (12.8% / 14.7%), *Abies concolor* (9.2% / 13.8%), *Abies lasiocarpa* (12.8% / 13.8%), *Pinus aristata* (12.8% / 11.9%), and *Pinus albicaulis* (1.8% / 1.8%). Overall there was a significant decline in percent of species composition that was live limber pine (-8.6% of stems, $P < 0.001$) and increase in live spruce-fir composition (+3.8%, $P = 0.01$) and other species such as *P. tremuloides* and *J. scopulorum* (+3.6%). However, in the Sangre de Cristo Mountains, there was a significant increase in limber pine (+2.4%, $P < 0.001$) while spruce-fir and other species decreased (-3.0%, $P = 0.009$ and 6.8%, $P = 0.004$, respectively) (Supplemental Table 5). Average live density of all species increased significantly over all plots from 614 stems ha^{-1} in 2004-07 to 740 stems ha^{-1} (+126 ± 25 stems ha^{-1}, $P = 0.01$), however significantly declined in Pole Mountain from 997 stems ha^{-1} in 2004-07 to 713 stems ha^{-1}in 2016-17 (-284 ± 81 stems ha^{-1}, $P = 0.01$). Live limber pine density decreased significantly over all plots from 361 stems ha^{-1} in 2004-07 to 310 stems ha^{-1} in 2016-17 (-51 ± 10 stems ha^{-1}, $P << 0.001$) and significant decreases in live limber pine density were also observed in Pole Mountain (-114 ± 44 stems ha^{-1}, $P = 0.01$) and the Shoshone NF (-99 ± 29 stems ha^{-1}, $P = 0.004$) (Table 2).

Live basal area for all species also declined significantly over all plots from 14.5 m^2 ha^{-1} in 2004-07 to 11.7 m^2 ha^{-1} in 2016-17 (-2.8 ± 0.7 m^2 ha^{-1}, $P < 0.001$) and there were significant decreases in Canyon Lakes (-7.3 ± 2.8 m^2 ha^{-1}, $P = 0.04$), Pole Mountain (-7.0 ± 2.5 m^2 ha^{-1}, $P = 0.03$), and Shoshone NF (-3.4 ± 1.5 m^2 ha^{-1}, $P = 0.04$). There was a significant decrease in basal area of live limber pine overall from 8.7 m^2 ha^{-1} in 2004-07 to 7.4 m^2 ha^{-1} in 2016-17 (-1.3 ± 0.4 m^2 ha^{-1}, $P = 0.002$) and in the Shoshone NF (-3.6 ± 1.5 m^2 ha^{-1}, $P = 0.03$) (Table 2).

Over all plots, the majority of live limber pine were in the 5.1-15.2 cm diameter class (39% in 2006-07, 41% in 2016-17) followed by 28% (2006-07) and 27% (2016-17) in the < 5 cm diameter class and 26% (2006-07 and 2016-17) in the 15.3-30.5 cm diameter class with the smallest proportion in the 30.5 cm diameter class (7% in 2006-07 and 2016-17). The number of live limber pine decreased overall from 3,625 in 2004-07 to 3,115 in 2016-17, with significant decreases in the <5 cm dbh class (-16.5%, $P = 0.001$), 5.1-15.2 cm class (-10.2%, $P = 0.001$), and 15.3-30.5 cm class (-17.0%, $P = 0.001$). Significant decreases were present in the < 5 cm diameter class in the Sangre de Cristo Mountains (-20.3%, $P = 0.007$) and Pole Mountain (-

53.6%, $P = 0.049$). In the 5.1-15.2 cm diameter class, significant decreases were observed at Pole Mountain (-21.1%, $P = 0.02$), Snowy Mountains (-14.8%, $P = 0.04$) and Shoshone NF (-17.3%, $P = 0.02$). In the 15.3-30.5 cm diameter class a significant decrease was observed in Shoshone NF (-42.4%, $P = 0.02$) and there was a significant increase in the >30.5 cm category in Sangre de Cristo Mountains (+10.8%, $P = 0.04$) (Supplemental Table 6).

Health status

Of the 3,701 limber pines > 1.3 m tall that were classified as healthy in 2004-07, 822 trees (22.2%) were declining/dying and 779 trees (21.1%) had died by the end of the study period (Figure 3, Supplemental Table 7). Of limber pine that declined during the study period, 19.5% (160 stems) were < 5 cm dbh, 43.4% (357 stems) were 5.1-15.2 cm dbh, 29.9% (246 stems) were 15.3-30.5 cm dbh, and 7.2% (59 stems) were > 30.5 cm dbh. Of limber pine that died during the study period, 23.0% (179 stems) were less than 5 cm dbh, 32.1% (250 stems) were 5.1-15.2 cm dbh, 35.3% (275 stems) were 15.3-30.5 cm dbh, and 9.6% (75 stems) were >30.5 cm dbh. The number of healthy limber pine in 2004-07 that advanced to declining/dying by 2016-17 was highest in Canyon Lakes (30.5%, 71 stems) and lowest at Laramie Peak (16.0%, 56 stems). The number of healthy limber pine in 2004-07 that were dead by 2016-17 was greatest at Pole Mountain at 37.9% (118 stems) and lowest in the Sangre de Cristo Mountains at 11.0% (73 stems). Significant increases were observed in the number of declining/dying limber pine in every subregion except Laramie Peak, Pole Mountain, Poudre South, and North Dakota. Additionally, the proportion of live limber pine with dead tops increased significantly from 8% (288 stems) to 12% (343 stems) during the study. Significant increases in the number of limber pine that went from living to dead over the study were seen in every subregion except Poudre South, Bighorn Mountains, and North Dakota (Figure 3, Supplemental Table 7).

Damage agents

Causes of mortality

Over all plots, MPB/Ips and WPBR killed 8.4% and 2.8% of limber pine >1.3 m, respectively with an additional 3.4% killed by combined damages of both agents (Supplemental Table 8). Of WPBR-killed limber, 39% showed damage from MPB/Ips; of MPB/Ips-killed limber 24% had WPBR infections (Supplemental Table 9). Of the 1,015 limber pine > 1.3 m tall that were standing dead in 2016-17 (26% of limber surveyed), 27% were killed by MPB/Ips, 11% were killed by WPBR, 14% were killed by combined effects of MPB/Ips and WPBR, and 38% died from other causes including cumulative damage from twig beetles (*Pityophthorus* spp., *Pityogenes* spp.), physical effects (frost cracks, lightning), animals girdling the bole, and/or dwarf mistletoe (*Arceuthobium cyanocarpum).* An additional 10% died from other causes but WPBR contributed to mortality (Figure 4). In addition to MPB/*Ips* and WPBR, the most common damage agent observed (biotic or abiotic) were twig beetles (*Pityophthorus* spp., *Pityogenes* spp.), which were found on 36% of declining/dying limber over all plots with the greatest damage observed in Poudre South (67%) followed by Montana (54%) and Snowy Mountains (48%).

Of the 272 limber pines killed by MPB/*Ips*, the majority (56%) fell into the 15.3-30.5 cm diameter class. Of the 159 limber pines killed by WPBR, the majority (> 90%) of infections were split between the < 5 cm diameter class (47.2%) and the 5.1-15.2 cm class (44.7%) (Supplemental Table 10). In sites with ≥ 20% WPBR incidence, 43% of limber pine killed by MPB/Ips had no detectable WPBR infections (Supplemental Table 9). The largest proportion (36%) of all pine species killed by MPB/*Ips* (n = 528) were attacked in 2009. Similarly, of the 343 limber pine killed by MPB/*Ips*, a peak occurred in 2009 when the largest proportion (43%)

of MPB/Ips-caused mortality occurred (Supplemental Figure 1). The largest portion of limber pine > 1.3 m tall killed by MPB/*Ips* occurred in the Shoshone NF (18%) and Canyon Lakes (12%) subregions.

WPBR incidence

Of the 106 sites, WPBR was not detected at 19 sites (18%) in 2004-07. However, four sites (4%) did not have WPBR-infected trees in 2004-07 but had gained infected trees during the study period. Incidence (number of live infected limber divided by number of live limber) was stable overall at 29.4% in 2004-07 and 25.7% in 2016-17 (-3.7 ± 0.5%, P = 0.16). Incidence increased significantly in Sangre de Cristo Mountains from 9.0% to 20.6% (+11.6 ± 1.2%, P = 0.01) but decreased significantly in Laramie Peak from 21.2% to 15.9% (-5.3 ± 0.7%, P = 0.03) and Pole Mountain from 65.0% to 50.0% (-15.0 ± 0.6%, P = 0.001) (Table 3). No WPBR infections were observed in North Dakota.

The proportion of WPBR infections decreased significantly overall plots in living limber pine < 5 cm dbh from 20.3% (214 stems) to 14.2 % (127 stems, P = 0.009) and in limber pine 5.1-15.2 cm dbh from 46.2% (481 stems) to 44.0% (406 stems, P = 0.009) (Supplemental Table 11). Similarly at Pole Mountain, significant decreases in WPBR infected live limber < 5cm dbh was observed from 28.7% (58 stems) to 13.9% (15 stems, P = 0.05) however a significant increase was observed in limber pine 5.1-15.2 cm dbh from 48.0% (97 stems) to 59.3% (64 stems, P = 0.01). Additionally at Pole Mountain, the total number of live infected limber pine (any diameter class) decreased significantly from 202 to 104 stems (P = 0.01). Incidence of WPBR in the 5.1-15.2 cm dbh class significantly decreased in the Bighorn Mountains from 33.8% (49 stems) to 28.2% (40 stems, P = 0.05) and in Montana from 44.8% (141 stems) to 44.2% (115 stems, P = 0.02). The incidence of WPBR significantly increased in the 15.3-30.5

cm dbh class in the Sangre de Cristo Mountains from 22.0% (13 stems) to 26.5% (37 stems) and Snowy Mountains from 8.5% (5 stems) to 17.7% (25 stems). Additionally in the Sangre de Cristo Mountains, WPBR incidence increased in live limber pine > 30.5 cm from 8.5% (5 stems) to 17.7% (25 stems). In 2004-07, 9.6% of declining/dying limber pine were infected with WPBR and in 2016-17 that number rose to 14.8%, though this difference was not statistically significant ($P = 0.16$).

WPBR severity

Using the rating system established by Six & Newcomb (2005, see Methods 2.3.3. White pine blister rust assessments), in 2011-13, 19 sites (24.1%) had no rust detected, 53 sites (67.1%) were lightly infected, 7 sites (8.9%) were moderately infected, and 0 sites were heavily infected. However by 2016-17, 17 sites (21.5%) had no infection, 28 sites (35.4%) had light infection, 29 sites (36.7%) had moderate infection, and 5 sites (6.3%) were heavily infected. Overall, WPBR severity increased significantly from 3.5 to 5.2 (+1.7 ± 0.2, $P < 0.001$) from 2011-13 to 2016-17, as did severity in every subregion except Snowy Mountains ($P = 0.45$) and Poudre South ($P = 0.39$) (data not collected in Sangre de Cristo Mountains, no WPBR in North Dakota). The range of severity ratings over all plots in 2004-07 was 0 - 6.5 which significantly increased to 0 - 11.4 in 2016-17 ($P < 0.001$), with the highest severity sites (11+ rating) occurring in the Shoshone NF and Bighorn Mountains (Table 3).

WPBR cankers

The distribution of cankers was highest in the middle third of the canopy where 44% of cankers occurred in 2011-13 and 41% in 2016-17 (no significant change). In Shoshone NF, the proportion of cankers that occurred in the lower third increased significantly from 25% in 2011-13 to 32% in 2016-17 (+7%, $P = 0.03$). Additionally over all plots, the proportion of cankers occurring in the lower third increased in trees < 5 cm dbh from 31% to 41% (P = 0.04) and in trees > 30.5 cm dbh from 30% to 34% (P = 0.02) between 2011-13 and 2016-17. No significant correlations were found between cankers occurring in any crown third and stand density or canopy closure. The average number of cankers per tree was 3.7 in 2004-07 and decreased to 3.3 in 2016-17, though not significantly (P = 0.6) (Supplemental Table 12). However, the average number of cankers per tree increased significantly in Laramie Peak from 1.5 in 2004-07 to 2.1 in 2016-17 (+0.6 ± 0.2, P = 0.03). In 2011-13, 13.4% of infected limber pine (> 1.3 m tall) had at least one stem canker in the lower third, this increased significantly to 17.6% in 2016-17 (+4.2 ± 0.1%, P = 0.001). Of trees with stem cankers, 48% were in the 5.1-15.2 cm diameter class, 28% in the 15.3-30.5 cm diameter class, 19% in the <5 cm diameter class and 5% in the >30.5 cm diameter class with no significant changes occurring from 2011-13 to 2016-17. The most common indicators of WPBR observed were swelling (80% of infected trees) followed by roughbark (79%) and sap production (79%). In the Bighorn Mountains, infected trees had significantly more rodent gnawing present (70% of trees) compared to other subregions (P = 0.001).

Other Damage Agents

The most common damage observed in live limber pine was from twig beetles (*Pityophthorus* spp., *Pityogenes* spp.) which decreased significantly from 35% in 2004-07 to 26% in 2016-17 (P = 0.001). Similarly, this trend was seen as twig beetle damage in WPBR-infected limber pine decreased from 39% in 2004-07 to 25% in 2016-17 (P = 0.003). The next most common damage observed was dead tops occurring in 8% of live limber pine in 2004-07 and increasing to 11% in 2016-17 (P = 0.048). Similarly, of WPBR-infected limber pine, dead tops increased significantly from 16% in 2004-07 to 29% in 2016-17 (P = 0.001). Limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*) was infrequently observed in 3% of live limber pine in both 2004-07 and 2016-17; of WPBR-infected limber pine, 2% had damage from mistletoe in all measurements.

Limber pine regeneration (< 1.3 m tall)

The density of limber pine regeneration in 2011-13 was 186 stems ha^{-1} (n = 1,354) and decreased to 180 stems ha^{-1} (n = 1,646) in 2016-17, though this change (-6 ± 5 stems ha^{-1}) was not significant (P = 0.09). Limber pine regeneration ranged from 0 - 2,454 stems ha^{-1} in 2011-13 and 0 - 2,249 stems ha^{-1} in 2016-17. In 2011-13, 5.3% of live stems < 1.3 m tall were infected with WPBR which decreased to 3.9% in 2016-17 though this change was not significant (-1.4 ± 1.5%, P = 0.3). Of the 80 sites measured in 2011-13 and 2016-17 (SOCO and ND excluded), 24% of sites had WPBR infected stems in 2011-13 which decreased to 18% in 2016-17 though this change was not significant (P = 0.26). In 2011-13, 1.0% of stems < 1.3 m tall were killed by WPBR and this number significantly increased to 2.6% in 2016-17 (+1.6 ± 0.9%, P = 0.03). Significant differences in regeneration density, WPBR incidence and mortality were not observed in any subregion (Table 4). All sites had ≥ 20% limber pine species composition, however 7% of sites had no regeneration of any tree species and 34% had no limber pine regeneration observed during the study period. The Bighorn Mountains had the highest percentage of sites (25%) with no regeneration of any species followed by the Shoshone NF (18%) and Canyon Lakes (13%). Similarly in the Bighorn Mountains, 58% of sites had no limber pine regeneration over the study period followed by 50% in Poudre South, 41% in the Sangre de Cristo Mountains, 38% in Canyon Lakes, 31% in Montana, 29% in both the Snowy Mountains and Shoshone NF, 14% in Laramie Peak, 13% in Pole Mountain, and 0% in North Dakota.

Significant ($P < 0.05$) correlations between WPBR incidence and mortality in regeneration (< 1.3 m tall) in 2011-13 and 2016-17 to stand and meteorological variables (Supplemental Table 2) revealed relationships with moderate ($R \geq |0.3|$) or weak associations ($|0.3| > R \geq |0.2|$) (Supplemental Table 15). In 2011-13 and 2016-17, WPBR incidence had a moderate positive relationship to relative humidity in September (R = 0.3, $P < 0.01$) and a weak positive relationship to the ratio of growing season precipitation to mean annual precipitation (R = 0.2, P = 0.03), precipitation in July (R = 0.2, P = 0.04), August (R = 0.2, P = 0.02), and the average (R = 0.2, P = 0.04) and minimum (R = 0.2, P = 0.04) temperature in December. Additionally, a weak negative relationship between WPBR incidence and December precipitation (R = -0.2, P = 0.04) was observed. In 2011-13 only, weak positive associations to WPBR incidence were observed for short wave radiation (R = 0.2, P = 0.01), water vapor pressure (R = 0.2, P = 0.01), the number of growing degree days (R = 0.2, $P < 0.01$), relative humidity in August (R = 0.2, P = 0.01), the average (R = 0.2, P = 0.04) and minimum (R = 0.2, P = 0.04) temperature in the coldest month (January), and the density of limber pine (live and total, R = 0.2, P = 0.02). A weak negative association between WPBR incidence and fertility index (R = -0.2, P = 0.03) was also observed in 2011-13. In 2016-17 only, WPBR incidence had weak negative relationships to the soil drainage index (R = -0.2, P = 0.04) and ratio of growing season degree days > 5°C to seasonal precipitation (R = -0.2, P = 0.04).

No significant correlations were observed for WPBR mortality to any variable in both 2011-13 and 2016-17 measurements. In 2011-13 only, weak positive associations to WPBR mortality were observed for short wave radiation (R = 0.2, P = 0.02), the number of frost free days (R = 0.2, P = 0.04), and basal area of all tree species (R = 0.2, P = 0.04). A weak negative association was observed between WPBR mortality and December precipitation (R = -0.2, P =

0.04). In 2016-17, moderate positive relationships were observed between WPBR mortality and water vapor pressure (R = 0.3, $P < 0.001$) and September relative humidity (R = 0.3, $P < 0.01$), while moderate negative relationships were observed to fertility index (R = -0.3, $P < 0.01$) and species composition that is 'Other Species' (R = -0.3, $P = 0.003$). Additionally in 2016-17, weak positive relationships were present between WPBR mortality and soil component frequency (R = 0.2, $P = 0.02$), growing degree days (R = 0.2, $P = 0.04$), growing season precipitation (R = 0.2, $P = 0.04$), precipitation in July (R = 0.2, $P = 0.03$) and August (R = 0.2, $P = 0.01$), and the density (live and total) of limber pine (R = 0.2, $P = 0.03$).

Site conditions associated with WPBR and MPB/*Ips* mortality

Stand characteristics showed significant ($P < 0.05$) correlations to WPBR incidence and mortality, but most had only weak or moderate association. Latitude, slope, and percent of ground cover consisting of vegetation had significant positive correlation to WPBR incidence in 2004-07 and 2016-17 but with weak association (R < 0.3, $P < 0.05$) (Supplemental Table 13). Additionally, longitude, slope, all species density, limber pine density, and spruce-fir species composition were positively correlated to WPBR mortality in 2016-17 but with weak association (R < 0.3, $P < 0.05$). Basal area of live limber pine was negatively correlated to WPBR mortality also with weak association (R < 0.3, $P < 0.05$). Species composition of 'Other Pines' was positively correlated to WPBR mortality in 2016-17 with a moderate association (R = 0.3, $P = 0.004$). As in Smith et al. (2013), a significant relationship was not observed between elevation and WPBR incidence in 2004-07 (R = -0.19, $P = 0.09$), in 2016-17 (R = -0.17, $P = 0.13$), or WPBR mortality (R = 0.09, $P = 0.42$) in 2016-17.

Climate data

Climate variable averages

Using averages of meteorological variables (Supplemental Table 1) from 1985-2016, the average length of the frost free period was 58 ± 2 days overall, with the longest period at 124 ± 1 days in North Dakota and the shortest at 47 ± 3 days in the Bighorns (Table 1). The average growing season precipitation was highest in North Dakota at 203 ± 1 mm and lowest in the Snowy Mountains at 65 ± 2 mm. The average annual moisture index (ratio of degree days >5°C to annual precipitation) was highest in North Dakota (599 ± 10) and lowest in the Bighorns (245 ± 11). The average seasonal moisture index (ratio of degree days > 5°C to seasonal precipitation) was highest in the Snowy Mountains (1738 ± 72) and lowest in the Sangre de Cristo Mountains (867 ± 41). The average temperature in the warmest month (July) was highest in North Dakota (21.3 ± 0.3°C) and lowest in the Bighorns (13.7 ± 0.5°C). The average temperature in the coldest month (January) was highest at Pole Mountain (-6.4 ± 0.3°C) and lowest in the Bighorns (-12.1 ± 0.5°C).

Climate correlations to WPBR incidence and mortality

Of correlations with significant p-value ($P < 0.05$), climate variables had weak to moderate associations to WPBR incidence (R < 0.4). Precipitation in May (R = 0.3, $P = 0.002$) and June (R = 0.4, $P = 0.0002$), and relative humidity in September (R = 0.3, $P = 0.002$) showed the strongest positive relationship with WPBR incidence in 2004-07 and 2016-17 of all variables. Growing season precipitation, precipitation in July, August, and September, and relative humidity in October showed positive associations with WPBR incidence in 2004-07 and 2016-17 but with weaker association (R < 0.3, $P < 0.05$). Relative humidity in June and mean annual precipitation showed a stronger association with WPBR incidence in 2016-17 (R = 0.3, $P = 0.03$)

than in 2004-07 (R = 0.2, P =0.01). Similarly, diffuse short wave radiation and 12-month moderate (or greater) drought frequency showed a moderate negative association with WPBR incidence in 2004-07 (R = -0.3, P = 0.006) but had a weaker association in 2016-17 (R = -0.2, P = 0.01). Derived short wave radiation showed a moderate negative association with WPBR incidence in both measurements (R = -0.3, P = 0.01) (Supplemental Table 13).

Climate variables with significant association to WPBR mortality in 2016-17 showed moderate (|R| > 0.3) or weaker relationships. Precipitation in July and percent species composition of the 'Other Pines' group both showed a positive association to WPBR mortality (R = 0.3, P < 0.004) in 2016-17. The frequency of 12-month moderate (or greater) drought showed a negative association to WPBR mortality (R = -0.3, P = 0.002) in 2016-17. Mean annual temperature, average number of growing degree days, the ratio of growing season precipitation to annual precipitation, average temperature in the warmest month (July), and the average temperature in the coldest month (January) showed positive, but weak association to WPBR mortality (R = 0.2, P < 0.05). The average number of degree days < 0°C, precipitation in January, November, and December, showed negative, but weak association (R = -0.2, P < 0.03) to WPBR mortality in 2016-17 (Supplemental Table 13).

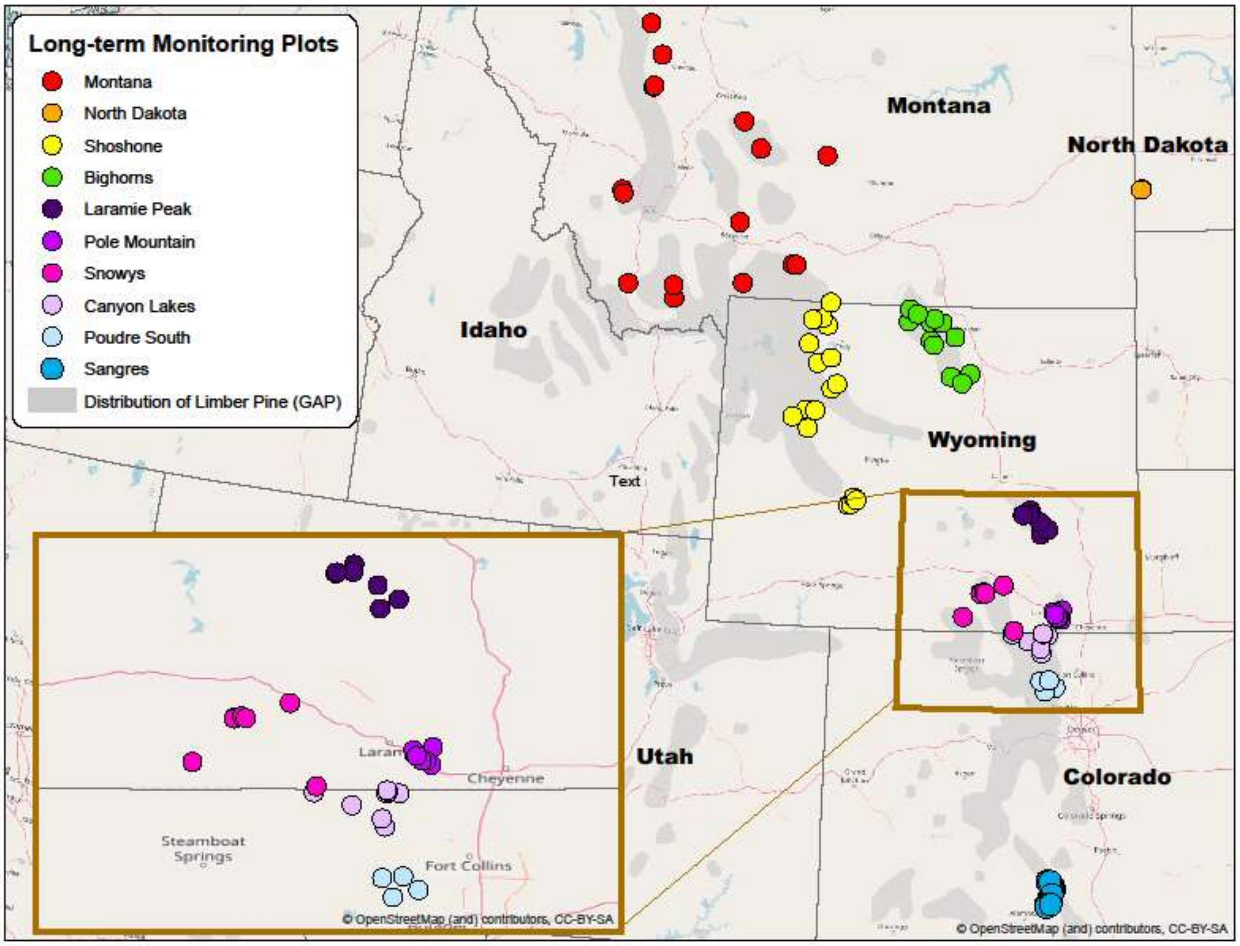

Figure 1 – Site Locations – 106 sites were measured in the U.S. Rocky Mountains and are denoted by subregion. Montana (MT) includes 16 sites, North Dakota (ND) includes 2 sites, Northern Wyoming (NOWY) includes a total of 29 sites in the Shoshone National Forest (17 sites) and Bighorn Mountains (12), the Colorado-Wyoming border (COWY) includes 34 sites total in Laramie Peak (7), Pole Mountain (8), Snowy Mountain Range (7), Canyon Lakes (8) and the southern Poudre Canyon /Rocky Mountain National Park ("Poudre South", 4) , Southern Colorado (SOCO) includes sites in the Sangre de Cristo Mountains (25). Limber pine distribution gathered from the USGS Gap Analysis Project (GAP).

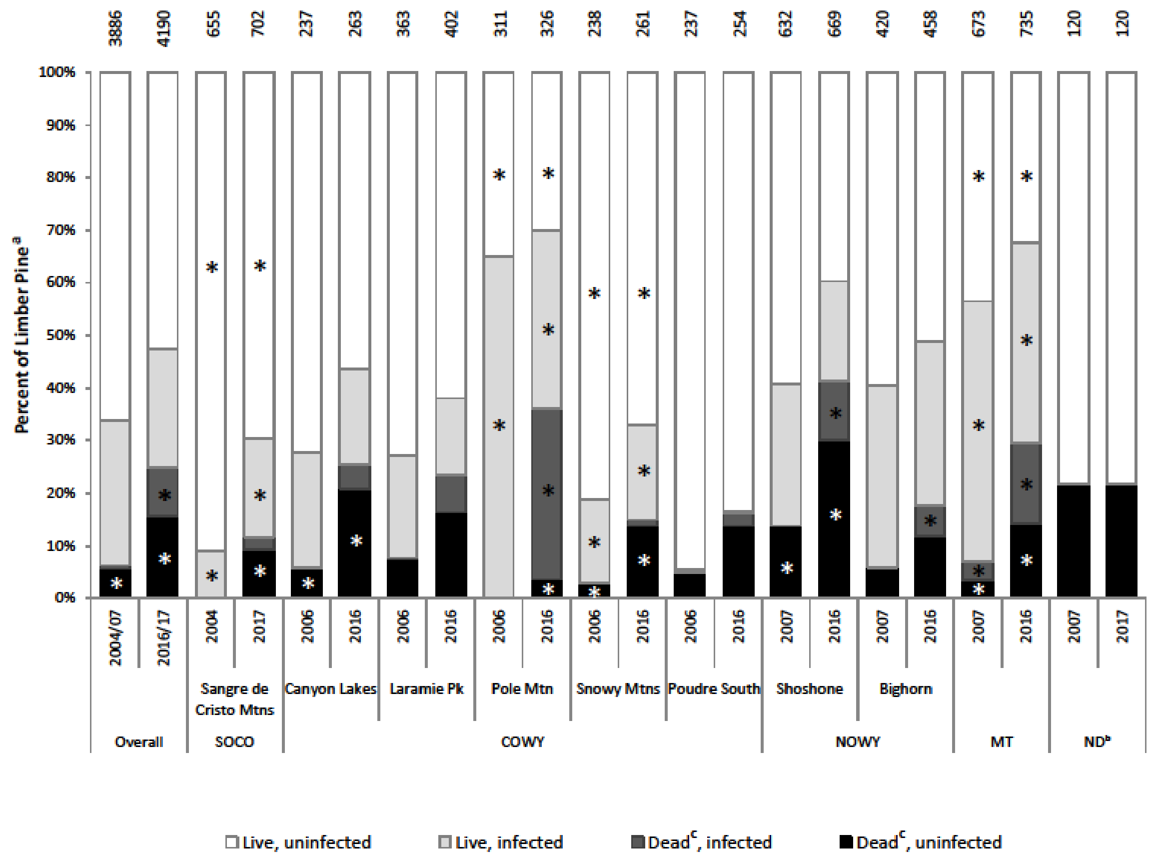

Figure 2 – Status of Limber Pine (> 1.3 m tall) and White Pine Blister Rust Infection (2004-07 to 2016-17) (a) dead from any cause, trees classified as "old dead" were not recorded in 2004-07; (b) ND had no rust infections (c) total number of limber surveyed listed at top of each bar. SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana. * Asterisks represent significant change ($P < 0.05$) using McNemar's test from 2004-07 to 2016-17 within subregions.

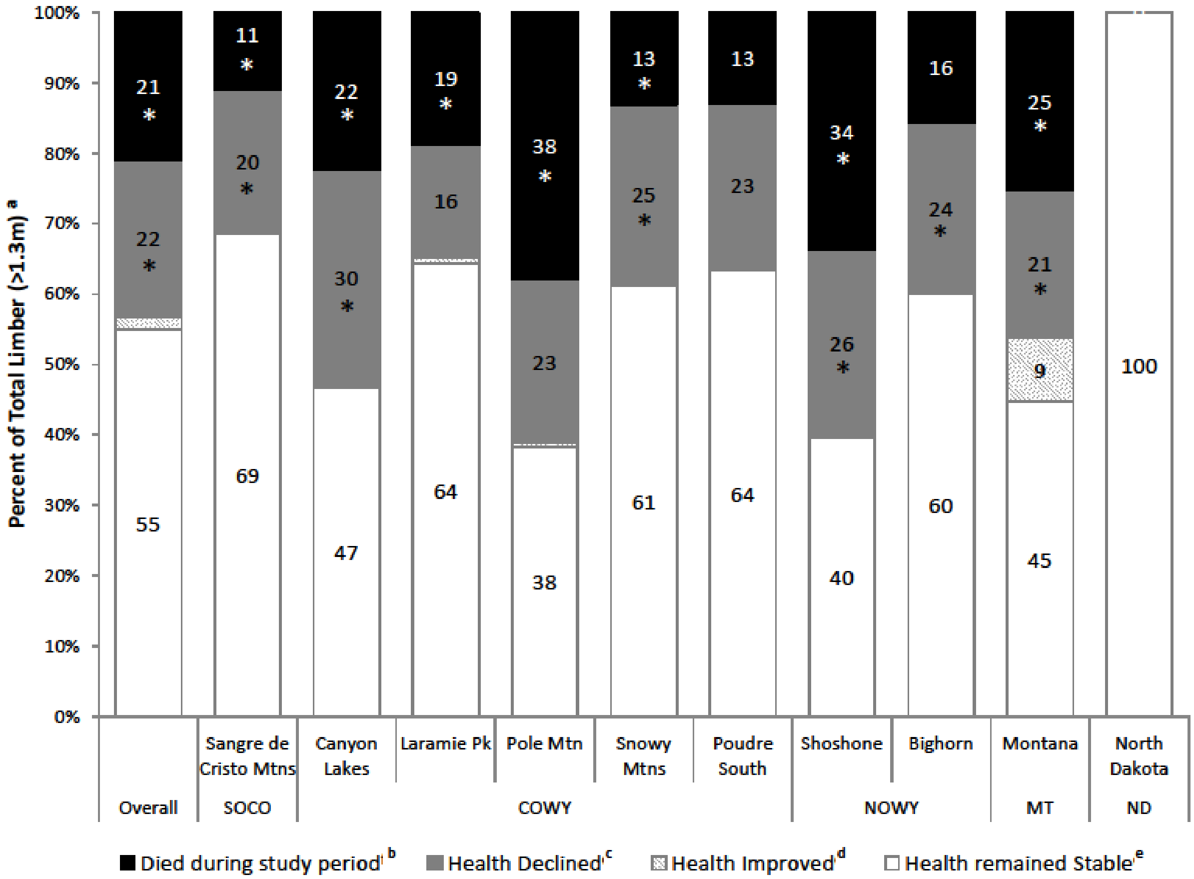

Figure 3 – Change in Limber Pine (> 1.3 m tall) Health Status 2004-07 to 2016-17
(a) Percent of total limber stems includes live and dead but does not include trees classified as old dead in 2004-07; (b) Died during study period: all trees that were alive at beginning of survey but died (from any cause) within the study period; (c) Health declined: damage accrued in the crown/stem throughout study period, trees in this category began as health status 1 and declined to status 2 (16-50% damage) or status 3 (>50% damage; (d) Health improved: status was greater than 1 (>16% damage to crown/stem) but reduced to a healthy status by end of survey period; (e) Health remained Stable: status of 1 (<15% damage to crown/stem) throughout survey period. SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota.

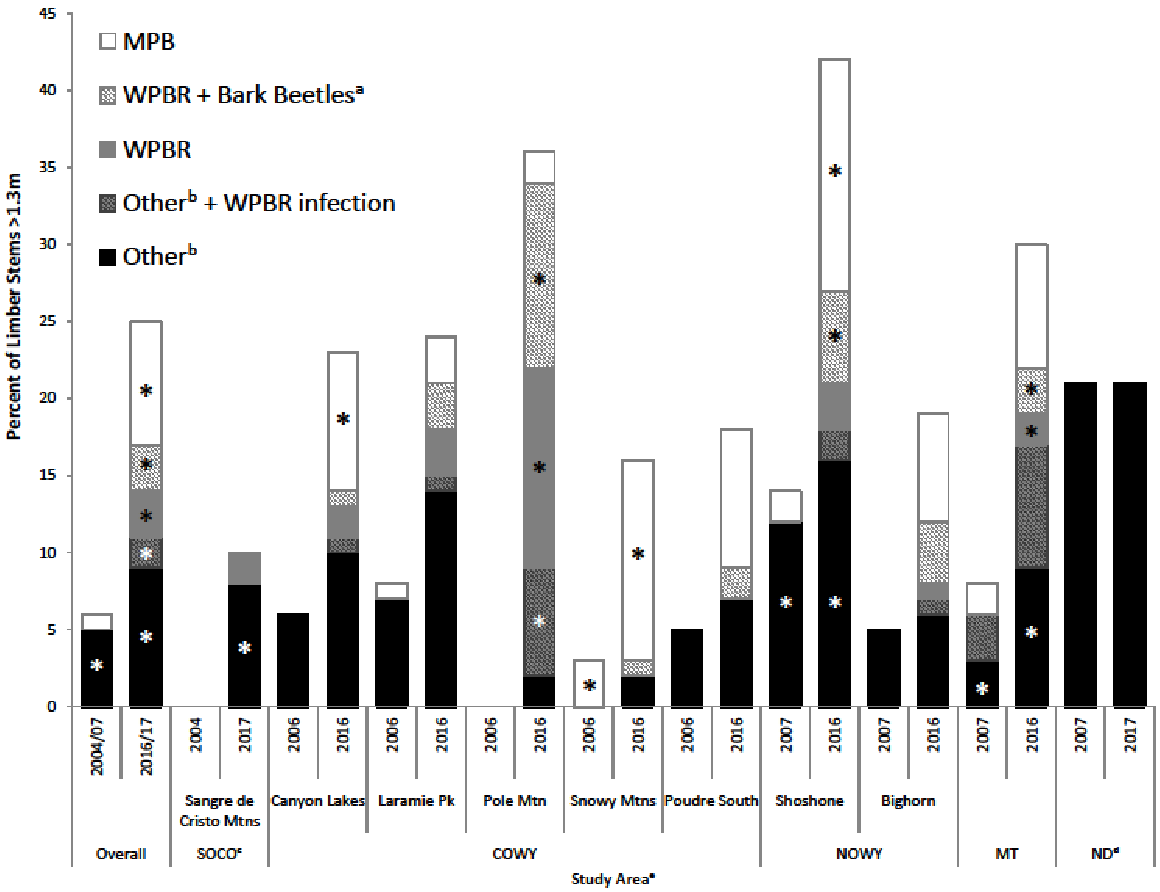

Figure 4 – Causes of Mortality in Limber Pine >1.3m tall (2004-07 to 2016-17) – (a) Both WPBR and bark beetles (including MPB/*Ips*) contributed considerably to mortality (b) Other damage agents contributing to mortality include (in descending order of damage caused): other bark beetles (*Pityophthorus* spp., *Pityogenes* spp., *Ips* spp.), limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*), animal/mechanical damage, physical effects (frost cracks, fallen tree damage, competition), and root disease; (c) SOCO sites installed in 2004 did not include dead trees, only 2017 data is displayed; (d) ND had no WPBR infections or bark beetle damages; (e) SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota. Asterisks (*) represent significant change ($P < 0.05$) using McNemar's test from 2004-07 to 2016-17 within subregion.

Table 1 – Site Characteristics for Study Areas

Study Area[a]		# of Sites	Elevation range (m)	Slope range (%)	Aspect range (°)	Avg growing season precipitation (mm) (mean ± SE)	Length of frost free period (days) (mean ± SE)	Avg temperature in January (°C) (mean ± SE)	Avg temperature in July (°C) (mean ± SE)
Overall		108	883 – 3593	0-77	0-350	103±3	58±2	-8.4±0.3	14.6±0.3
SOCO	**Sangre de Cristo Mtns**	27	2810 - 3593	0-55	0-315	124±2	54±3	-8.4±0.4	13.9±0.5
COWY	**Canyon Lakes**	8	2460 - 2700	3-58	20-335	93±4	61±4	-6.7±0.4	14.9±0.4
	Laramie Pk	7	2308 - 2570	2-35	0-350	94±5	68±3	-7.8±0.4	15.6±0.4
	Pole Mtn	8	2328 - 2648	5-30	90-350	119±4	73±3	-6.4±0.3	15.4±0.5
	Snowy Mtns	7	2531 - 2734	5-39	53-340	65±2	54±3	-7.7±0.3	14.9±0.3
	Poudre South	4	2522 - 3122	10-35	180-240	120±7	60±11	-7.1±1.2	14.3±1.6
NOWY	**Shoshone**	17	1840 - 2711	3-40	12-320	79±4	52±5	-9.0±0.8	14.2±0.6
	Bighorn	12	2268 - 2791	10-43	0-340	81±2	47±3	-12.1±0.5	13.7±0.5
MT		16	1460 - 2391	1-77	157-320	116±7	61±6	-7.5±0.5	14.8±0.9
ND		2	884	32-77	74-216	203±1	124±1	-9.0±0.2	21.3±0.3

SE represents standard error
[a]SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota

Table 2 – Density and Basal Area of Surveyed Trees (> 1.3 m tall)

Study Area [a]		Average Live Density (stems • ha^{-1})						Average Live Basal Area (m^2 • ha^{-1})					
		All tree spp.			Limber pine			All tree spp.			Limber pine		
		04-07	16-17	Change ± SE	04-07	16-17	Change ± SE	04-07	16-17	Change ± SE	04-07	16-17	Change ± SE
Overall		614	740	**126±25**	361	310	**-51±10**	14.5	11.7	**-2.8±0.7**	8.7	7.4	**-1.3±0.4**
SOCO [b]	Sangre de Cristo Mtns	--	--	--	261	247	-14±10	--	--	--	11.0	11.3	0.2±0.2
COWY	Canyon Lakes	962	880	-82±62	300	262	-38±18	18.2	10.9	**-7.3±2.8**	2.9	2.5	-0.4±0.4
	Laramie Pk	1161	1035	-126±139	515	474	-42±36	14.9	13.2	-1.7±1.4	4.1	3.7	-0.4±0.4
	Pole Mtn	997	713	**-284±81**	418	274	**-144±44**	17.3	10.3	**-7.0±2.5**	4.8	2.8	-2.0±1.0
	Snowy Mtns	523	537	14±23	355	321	-34±16	12.3	10.7	-1.6±1.1	10.9	8.9	-2.0±1.2
	Poudre South	904	969	65±99	605	568	-38±24	21.8	18.1	-3.7±3.5	14.4	11.6	-2.8±2.1
NOWY	Shoshone	508	452	-56±51	346	247	**-99±29**	10.6	7.2	**-3.4±1.5**	8.4	4.8	**-3.6±1.5**
	Bighorn	709	749	40±36	354	338	-16±36	17.0	17.2	0.2±2.3	12.6	11.7	-0.9±2.2
MT		891	826	-65±46	410	341	-69±26	13.4	12.5	-0.9±1.3	6.9	5.5	-1.4±1.2
ND		1211	1211	0±0	506	506	0±0	7.5	7.5	0±0	5.0	5.0	0±0

[a] SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota
[b] In SOCO, only white pines were measured for density and basal area
SE represents standard error
Bolded values indicate significant change ($p < 0.05$) using paired T-test from 2004-07 to 2016-17 within subregion

Table 3 – Incidence and Severity of White Pine Blister Rust in Limber Pine (>1.3 m tall)

Study Area [a]		# Live WPBR Stems (# cankers)		Incidence [b] (%)					Severity [c]					
				Mean (range)				**Change ± SE**	**Mean ± SE** (range)				**Change ± SE**
		04-07	**16-17**	**04-07**		**16-17**			**11-13**		**16-17**		
Overall		1070 (2150)	809 (2714)	29.4	(0 – 92.9)	25.7	(0 – 92.9)	-3.7±0.5	**3.5**	(0 – 6.5)	**5.2**	(0–11.4)	**1.7±0.2**
SOCO	Sangre de Cristo Mtns	59 (88)	128 (392)	**9.0**^{1}	(0 – 60.0)	**20.6**^{1}	(0 – 71.7)	**11.6±1.2**	n/a		n/a		
COWY	Canyon Lakes	52 (88)	35 (130)	23.3^{123}	(0 – 88.9)	17.9^{123}	(0 – 81.5)	-5.4±1.6	**4.5**	(0 – 6.3)	**5.9**	(0 – 6.8)	**1.4±0.5**
	Laramie Pk	71 (50)	49 (103)	**21.2**^{12}	(0 – 35.5)	**15.9**^{123}	(2.0 – 37.7)	**-5.3±0.7**	**3.6**	(0 – 4.6)	**7.0**	(0-10.4)	**3.4±0.6**
	Pole Mtn	202 (393)	104 (445)	**65.0**^{3}	(58.3–73.7)	**50.0**^{3}	(53.8–73.7)	**-15.0±0.6**	**3.7**	(2.5-5.3)	**6.9**	(4.3-9.7)	**3.2±0.8**
	Snowy Mtns	38 (75)	42 (118)	16.5^{12}	(0 – 47.1)	18.9^{123}	(0 – 40.0)	2.4±1.0	1.9	(0 – 4.0)	2.6	(0 – 4.0)	0.7±0.3
	Poudre South	1 (2)	1 (2)	0.4^{1}	(0 – 9.1)	0.5^{12}	(0 – 9.1)	0.1±0.1	1.0	(0 – 1.0)	2.0	(0 – 2.0)	1.0±0.2
NOWY	Shoshone	170 (403)	111 (400)	31.2^{12}	(0 – 86.7)	28.3^{123}	(0 – 82.4)	-2.9±1.4	**3.4**	(0 – 6.5)	**6.6**	(0 –11.0)	**3.2±0.6**
	Bighorn	145 (589)	128 (587)	36.7^{23}	(4.3 – 92.9)	34.0^{23}	(6.1 – 92.9)	-2.7±0.8	**3.5**	(1.0–5.0)	**6.2**	(1.0-11.4)	**2.7±0.6**
MT		332 (462)	211 (537)	53.0^{23}	(0 – 91.2)	40.7^{123}	(0 – 91.4)	-12.3±1.3	**3.5**	(0 – 5.6)	**6.2**	(0 – 8.2)	**2.7±0.4**

[a] SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana; no WPBR infections observed in North Dakota.

[b] Number of infected limber pine (>1.3m tall) out of live limber pine (>1.3m tall); Superscripts 1-3 denote significant groupings of subregion incidence within sampling (04-07 or 16-17) determined by ANOVA with Tukey adjustment

[c] Six and Newcomb (2005) rating system for 2011-13 and 2016-17 measurements, data not recorded in 2004-07. Only cankers on living trees were included in calculations. Severity scores range from 0-18: 1-4 (light infection), 5-8 (moderate infection), and 9+ (heavily infected).

Bolded values indicate significant change (p < 0.05) using paired T-test within subregion

Table 4 – Density of Limber Pine Regeneration (< 1.3m tall) and White Pine Blister Rust (2011-13 [a] to 2016-17)

Study Area [b]		Total limber stems (<1.3m)		Average Density (stems · ha^{-1})			WPBR Incidence [d] (%)					WPBR Mortality [e] (%)				
							11-13		16-17			11-13		16-17		
		11-13	16-17	11-13	16-17	Change ± SE	n	Mean	n	Mean	Change ± SE	n	Mean	n	Mean	Change ± SE
Overall [c]		1354	1646	186	180	-6±5	64	5.3	39	3.9	-1.4±1.4	**16**	**1.0**	**43**	**2.6**	**1.6±0.9**
SOCO	**Sangre de Cristo Mtns**	--	177	--	70	--	--		7	4.5		--		3	2.3	--
COWY	**Canyon Lakes**	118	85	159	114	-44±13	5	9.7	3	7.1	-2.6±1.9	1	2.9	1	2.4	-0.5±1.1
	Laramie Pk	343	342	615	567	-48±6	6	3.6	1	0.5	-3.1±7.3	1	0.3	0	0	-0.3±0.6
	Pole Mtn	135	215	182	289	108±13	14	12.7	7	11.5	-1.1±4.7	6	3.4	13	7.5	4.0±2.7
	Snowy Mtns	71	59	101	83	-18±19	2	3.3	0	0	-3.3±4.6	0	0	2	1.4	1.4±1.9
	Poudre South	51	66	137	178	40±4	0	0	0	0	0	0	0	0	0	0
NOWY	**Shoshone**	224	287	142	182	40±17	3	2.4	3	5.0	2.6±7.9	1	0.2	1	0.4	0.2±0.8
	Bighorn	45	84	40	75	35±7	4	4.2	3	1.0	-3.2±3.9	0	0	6	6.7	6.7±4.2
MT		367	504	247	339	92±10	30	5.3	22	2.4	-3.0±1.1	7	1.0	20	2.5	1.5±0.7
ND		--	4	--	22	--	--		0	0	--	--		0	0	--

[a] Whole plot counts of limber pine regeneration were not taken in 2004-07.
[b] SOCO: Southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: Northern Wyoming, MT: Montana, ND: North Dakota
[c] SOCO and ND plots were not visited in the 2011-13 measurement.
[d] Incidence was calculated as the number of infected limber pine (>1.3m tall) out of the number of live limber pine (<1.3m talll).
[e] Mortality was calculated as number of limber pine <1.3m tall killed by WPBR divided by total number of limber pine <1.3m tall.
SE represents standard error
Bolded values indicate significant change (p < 0.05) using paired T-test within subregion

CHAPTER 4: DISCUSSION & CONCLUSION

Over the course of this time series analysis, nearly half of the limber pines surveyed declined or died due to effects of bark beetles and WPBR. White pine blister rust incidence varied significantly between and even within mountain ranges. Incidence was stable in most subregions, declined in Pole Mountain and Laramie Peak, and increased in the Sangre de Cristo Mountains (Table 3). Though the number of infected, live trees did not significantly change in subregions with stable disease incidence, a large proportion of limber pines died across all plots and WPBR severity on remaining trees significantly increased in most subregions. However, stable or decreased incidence rates in all subregions, except Sangre de Cristo Mountains, may not accurately reflect the occurrence of new WPBR infections as infected limber pine that died were no longer included in incidence calculations. This decrease in the number of live, infected trees may have masked the number of new WPBR infections if new infections were occurring at the same (incidence is stable) or a slower (incidence decreased) rate than infected trees were dying.

Overall, the combination of the recent MPB epidemic, ongoing damages from twig beetles, and intensification of WPBR infections resulted in a substantial health decline of the limber population. The high frequency of declining (22%) or dead (21%) limber pine during the 9-13 year study period is alarming; especially due to the long maturation period of limber pine (about 50 years, Schoettle 2004). As changing climates could potentially increase WPBR and bark beetle activities (Larson et al. 2011, Kipfmueller et al. 2002), continued monitoring and development of restorative management plans for heavily impacted areas where limber pine is a climax species and proactive management in healthy stands will be necessary to preserve this species.

WPBR incidence

WPBR incidence among live limber pine over all plots was stable or decreased during the study period, except in the Sangre de Cristo Mountains where incidence increased; however this was coupled with mortality of infected trees indicating a continuing infection of new trees over the study period. Incidence values between and even within mountain ranges varied widely as noted in previous surveys (Kearns & Jacobi 2007, Cleaver et al. 2015). Those surveys also assessed Canyon Lakes, Laramie Peak, Pole Mountain, Snowy Mountains, and Shoshone NF subregions for WPBR incidence, though sites were generally not overlapping. Kearns & Jacobi (2007) evaluated areas in 2002-2004, a few years before our initial survey of these areas and Cleaver et al. (2015) surveyed in 2011-12. In Canyon Lakes, a higher incidence was captured in our study (23% in 2004-07 and 18% in both 2011-13 and 2016-17) as compared to the 4% and 8% found in 2002-04 and 2011-12, respectively. As shown from these comparisons, WPBR incidence varied greatly between and even within geographic ranges. Cleaver et al. (2015) and Kearns & Jacobi (2007) had more sites than our study, and thus, due to increased sample size likely had a higher resolution of WPBR incidence values in these areas. Incidence values for Laramie Peak area were consistent across all five measurements (about 20%) generally showing disease stability in this subregion. Pole Mountain, however, which was surveyed heavily including all 3 surveys, had varied incidence values. In 2002, incidence of WPBR in live trees was 30% (Kearns & Jacobi 2007), in 2006 was 65% (Burns et al. 2011), dropped to 34% in 2011 (Cleaver et al. 2015), but was 56% and 50% in this survey’s 2012 and 2016 measurements, respectively. The discordance of incidence values across these studies indicates the surprising variability of WPBR incidence across stands even within a region.

The comparison between Pole Mountain and the Snowy Mountains, in particular, serves as a case study for describing the variability in WPBR incidence between adjacent mountain ranges. Though these subregions are within 80 miles of each other, they have significantly different WPBR incidence values ($P = 0.001$). More than 50% of live limber pine > 1.3 m tall in Pole Mountain had WPBR infections in each measurement whereas in the Snowy Mountains WPBR infections were less than 20%. It is likely that climatic factors, such as high humidity and sustained wind events, account for increased incidence and severity at Pole Mountain in comparison to the nearby Snowy Mountains. However, correlation analyses between climate variables and WPBR incidence and mortality yielded few meaningful results. It is possible that climate data obtained from the PRISM climate group and Daymet U.S. Data Center for the GPS coordinates of each plot does not possess the resolution necessary to capture the microclimate dynamics occurring at the stand and individual tree level. Concurring with Cleaver et al. (2015), in this study significant correlations to WPBR incidence were observed with weak to moderate ($R < |0.4|$) association with precipitation measures such as 12-month moderate or greater drought frequency, precipitation in May and June, and relative humidity in September. Climate variability even within close mountain ranges supports the development of integrated management plans tailored to local geographic areas. Range specific long-term studies allow us to correlate changes in areas with specific climate and geography for projecting future trends and appropriate management practices for areas ahead of the disease front.

Decreasing WPBR incidence in two subregions, Pole Mountain and Laramie Peak, coincided with significant increases in WPBR severity and mortality (all causes). At Pole Mountain, significant increases in mortality associated with WPBR (exclusively, with bark beetles, or in conjunction with other causes) resulted in 38% of limber pine mortality over a ten-year period. In addition, 23% of limber pines at Pole Mountain were classified as declining or dying because of WPBR and/or bark beetle affects. It is likely that the high limber pine mortality observed at Pole Mountain contributed to a decrease in incidence, as fewer live trees are present on site to become infected. Laramie Peak underwent less dramatic changes with 16% of limber pine declining or dying and 19% having died in a ten-year period due to a combination of WPBR and bark beetle damages (Figure 3, Supplemental Table 7). The significant decreases in WPBR incidence in these subregions is not to be misunderstood as reduction of disease impacts, as severity of WPBR and limber pine decline in both subregions is considerable.

WPBR incidence rates were stable in the remaining subregions except for a significant increase in the Sangre de Cristo Mountains of Southern Colorado. This may indicate that live trees in this area will continue to accumulate infections until incidence rates stabilize, as our data showed in more northern areas where WPBR has been present for decades. Regardless of the length of time WPBR has been present in a region, infection severity may continue to intensify long after incidence rates stabilize. In subregions north of the Sangre de Cristo Mountains, the stabilization of infection rates suggests that the majority of susceptible trees have been infected, however intensification of WPBR infections may continue for many years. Limber pine in the Sangre de Cristo Mountains share an ecological niche with another high-elevation white pine, Rocky Mountain bristlecone pine (*P. aristata*). Though they occupy many of the physical sites and ecological roles of limber pine, bristlecone pines display an unusually high resistance to WPBR (Bingham 1972, Childs & Bedwell 1948, Hoff et al. 1980, Vogler 2005, Schoettle et al. 2011, Schoettle et al. 2014). This was observed in this survey, as no WPBR infections were observed on bristlecone pine even areas with relatively high WPBR incidence in Sangre de Cristo Mountains (up to 72%). Long-term surveys in southern Colorado and New Mexico are currently underway in order to determine the effects of the pathogen on these southern populations.

Correlations were evaluated between meteorological and stand variables in relation to WPBR incidence though significant correlations showed moderate or weaker association. In agreement with previous studies (Cleaver et al. 2015, Kearns & Jacobi 2007), a weak positive association between latitude and WPBR incidence was observed ($R = 0.2$, $P = 0.03$). Similarly, moderately positive associations between WPBR incidence and mean precipitation in May ($R = 0.3$, $P = 0.002$) and June ($R = 0.3$, $P = 0.0004$) and relative humidity in June ($R = 0.3$, $P = 0.01$) were observed, while WPBR incidence was negatively associated with a 12-month moderate or greater drought frequency ($R = 0.3$, $P = 0.01$) as observed in Cleaver et al. (2015). As suggested in previous studies, these findings indicate that humidity plays a role in WPBR infection rates (Hirt 1942, Van Arsdel et al. 1956, Cleaver et al. 2015). Of variables with significant correlations, the highest R values had only moderate associations ($0.3 > R < 0.4$) to WPBR incidence. Additionally, the variability between stands within subregions, as witnessed in high infection areas such as Pole Mountain, may limit our ability to effectively and accurately correlate these variables.

Over the study period, the proportion of WPBR infections occurring in trees with < 15.2 cm (< 6”) dbh decreased (Supplemental Table 11) as did the overall number of live limber pine in those diameter classes (Supplemental Table 6). Further, 90% of WPBR-killed trees were <15.2 cm (< 6”) dbh. It is likely that the decrease in WPBR infections in trees < 15.2 cm dbh was the result of fewer live trees on sites for the pathogen to infect, especially in areas such as Pole Mountain where a 53% decrease in live limber pine < 5cm dbh and a 21% decrease in 5.1-15.2 cm dbh was observed. In the Sangre de Cristo Mountains, significant increases in WPBR infections were observed in live limber pine > 15.3 cm dbh. As 20% of live limber pine < 5 cm dbh were lost in this region and an 11% increase in the proportion of live limber pine > 30.5 cm was observed, these increases in larger diameter trees may be attributed to there being fewer small trees on site to infect. Six & Adams (2007) showed that greater WPBR severity in whitebark pine was correlated to the likelihood of MPB attack. Our data showed that MPB/Ips favors trees in the 15.3-30.5 cm diameter class (56% of MPB/*Ips*-killed trees) as established previously (Gibson et al. 2008, Klutsch et al. 2009) and in subregions with high MPB/Ips damage, such as the Snowy Mountains, a significant increase in WPBR incidence in trees from 15.3 – 30.5 cm dbh was observed +9%, P = 0.04).

WPBR severity

Though the number of live, WPBR infected trees did not increase in Wyoming and Montana, disease severity is increasing in all subregions regardless of incidence rates. The increase in severity was noted at both the individual tree and stand levels, with the number of stem cankers occurring in the lower third of the stem, Six & Newcomb severity rating, and the amount of dead top damages increasing significantly over the 9-13 year period. The dramatic increase in severity throughout the study areas was demonstrated in the increase in stem cankers, specifically stem cankers in the lower third of the bole in every subregion regardless of incidence or severity level. Overall the number of infected limber with a stem canker in the lower stem third significantly increased from 13.4% in 2011-13 to 17.6% in 2016 (+4.2%, P = 0.001). Some areas had even greater increases in presence of basal stem cankers such as Pole Mountain (+10.5%, P = 0.08), Bighorn Mountains (+8.0%, P = 0.048), and Montana (+8.0%, P = 0.2), however this increase was only statistically significant in the Bighorns (Supplemental Table 12).

Cankers lower on the bole are much more likely to girdle and kill the entire tree, thus this observed increase suggests a higher likelihood of mortality for such trees.

Moreover, the stand level average severity ratings (Six & Newcomb, 2005) not only increased significantly in most subregions (except the lower incidence areas of Poudre South and Snowy Mountains), but nearly doubled in all except Canyon Lakes. Overall, there was a 28% increase from lightly to moderately infected stands and a 6% increase from moderate to severely infected stands. In areas such as Montana and northern Wyoming, where the disease has been present for over five decades, severity values nearly doubled from 3.5 in 2011-13 to 6.2 in 2016 in Montana, 3.4 to 6.6 in Shoshone NF, and 3.5 to 6.2 in the Bighorn Mountains. Additionally, the highest disease severity in the study was witnessed in the Shoshone NF and Bighorns Mountains with each range having multiple sites with stand severities > 11. Conversely, severity scores were lower in areas with more recent discovery of WPBR such as the Snowy Mountains (2.6) and Poudre South (2.0) (data not collected in Sangre de Cristo Mountains). These data suggest that both areas with the oldest presence of WPBR infections and areas closer to the disease front are increasing in disease severity. This is evidence that though WPBR has been in these areas for decades and incidence may have stabilized, increasing severity is still contributing to the mortality of limber pine. Over all plots, the intensification of WPBR severity is highlighted in the significant increases in declining, dying, and dead limber pine over the relatively short study period.

Health trends and mortality

A significant proportion of the limber pine population (> 1.3 m tall) went from healthy to declining or dying during the study period in all subregions except Laramie Peak, Pole Mountain, and Poudre South. It is possible that in Laramie Peak and Pole Mountain the number of declining/dying limber pine was not significant over the study period because a large proportion of trees in those subregions were already declining/dying when the study began, mostly due to WPBR and bark beetle damages. Of limber pines that were declining/dying, WPBR (52%) and twig beetles (37%) contributed significantly to damages that resulted in decreased health status (increased proportion of crown damaged). In Poudre South, fewer trees were declining or dying possibly because of the low WPBR incidence in that subregion.

A noticeable decline was observed in limber pine populations across the U.S. Rocky Mountains as 12-38% of healthy limber pine died and an additional 16-30% went from healthy to declining or dying, over the 9-13 year study. White pine blister rust was a substantial contributor to this mortality with significant increases in dead, infected limber pine overall, as well as in Pole Mountain, Shoshone NF, Bighorn Mountains, and Montana (Figure 2). In particular, limber pine at Pole Mountain had the greatest impacts from WPBR, in conjunction with bark beetles and other damages, accounting for mortality in 38% of trees. Of limber pine classified as declining/dying during the study period, 52% had WPBR infections and 37% had damages from twig beetles. Together these two damage agents contributed almost exclusively to the 11% of live limber with dead tops, a known contributor to mortality (Fazio & Krumpe 1999). Though little mortality was attributed to twig beetles specifically, in conjunction with the increase in severity of WPBR, damage by these beetles contributed to the decline of healthy trees over the study period as 22% of WPBR-infected trees had measurable twig beetle damage.

Interestingly, though the Shoshone NF and Bighorn Mountains did not have significantly different WPBR incidence values in either 2004-07 or 2016-17 (Table 3), the mortality rate from WPBR was significantly higher in Shoshone NF (3.1%) than in the Bighorn Mountains (0.7%) (P = 0.01) (Supplemental Table 8). In the Shoshone NF, the majority of WPBR-killed limber pine were in the 5.1-15.2 cm dbh class (61%) whereas the majority in the Bighorns were <5 cm dbh class (50%) (Supplemental Table 10). Moreover, the proportion of living limber pine in these diameter classes between the two subregions was not significantly different (Supplemental Table 6). This is likely due to the significant increase in the number of stem cankers in the lower third that was observed in the Bighorn Mountains (+8%, P = 0.048) whereas a smaller and non-significant increase was observed in Shoshone NF (+5%, P = 0.22) (Supplemental Table 12). However, the average number of cankers per tree, total number of cankers (stem or branch) and severity ratings for both subregions were not significantly different in any measurement. Over all sites, 90% of WPBR mortality occurred in diameters < 15.2 cm (< 6”) and in the Sangre de Cristo Mountains the few limber pine killed by WPBR were of the smaller (< 15.2 cm) diameter classes. These data support that smaller diameter trees succumb to the pathogen at a higher rate than large diameter trees, likely due to the shorter distance the pathogen must grow from where infection occurs on the needles to girdling of the stem (Burns et al. 2008).

A large portion of the recent MPB epidemic occurred during the study period (2006-2013) and peaked during the middle of the study (2009), allowing us to capture information regarding WPBR infections before and after bark beetle mortality (Supplemental Figure 1). Overall, MPB/Ips was the causal agent of mortality for 8.4% of limber pine > 1.3 m tall with the greatest impacts in Canyon Lakes, Snowy Mountains, and Shoshone NF, though these numbers may be underestimated as this time series did not assess cause of death for standing dead trees in 2004-07. Our data supports that MPB/Ips favors larger diameter trees with the majority of MPB/Ips-killed trees (56%) belonging to the 15.3-30.5 cm diameter class, as compared WPBR where the majority of mortality occurred in diameters < 15.2 cm. Additionally, limber pine >

30.5 cm in diameter made up a significant portion of MPB/*Ips*-killed trees in Poudre South (31%), Bighorn Mountains (37%) and Montana (20%) (Supplemental Table 10).

The accumulation of decline and mortality from both bark beetles and WPBR is striking over this short period, as MPB epidemics have peaked in the past and will continue to peak in the future. Additionally, WPBR is now a permanent part of the North American forest ecosystem and thus long-term management of this pathogen is needed. The combination of these two damage agents is worth noting as bark beetles can kill potentially WPBR-resistant trees (Burns et al 2008). In sites with >20% WPBR incidence, 43% of MPB/*Ips* killed limber pine were uninfected with WPBR overall (Supplemental Table 9). This trend was also observed in the Bighorn Mountains (65%) and in Montana (48%) implying that large MPB/*Ips* epidemics could potentially alter the favorable gene pool of WPBR resistance on the landscape. With climate models predicting a warmer climate potentially more suitable to WPBR infections (Rehfeldt et al. 2008**)** and more frequent and severe MPB epidemics to occur in the future, the preservation of WPBR-resistant limber pine will be critical to preservation of the species (Schoettle & Sniezko 2007).

Species composition was recorded before and after a significant portion of the limber pine population was killed by the recent MPB epidemic and ongoing WPBR infections, allowing for insight on how forest landscapes are being affected by these biotic factors. Live limber pine composition significantly decreased over all plots combined (-8.6%, $P < 0.0001$) as both the 'Spruce-Fir' category (Douglas-fir, subalpine fir, white fir, and Engelmann spruce) and 'Other species' category (Rocky Mountain juniper and quaking aspen) increased significantly (+3.8%, $P = 0.01$ and +3.6%, $P = 0.03$, respectively) (Supplemental Table 5). Conversely, in the Sangre de Cristo Mountains, limber pine composition increased significantly (+2.4%, $P = 0.01$) whereas

‘Spruce-fir’ and ‘Other species’ underwent a significant decrease (-3.0%, $P = 0.009$ and -6.8%, $P = 0.004$, respectively). Decreases in live limber pine composition were also observed at Pole Mountain (-3.4%, $P = 0.01$), Shoshone NF (-13.5%, $P = 0.004$), and Montana (-4.8%, $P = 0.04$), however no significant increases in live trees of any other species group was observed. Similarly, a significant decrease in ‘Other pines’ (lodgepole and ponderosa pines) was observed at Canyon Lakes (-7.2%, $P = 0.04$), likely due to bark beetle effects, as mortality from MPB/Ips in this subregion was high (23% of ‘Other pines’ stems). Limber pine is considered an early seral species outcompeted in moderate environmental conditions by species such as subalpine fir, Engelmann spruce, and Douglas-fir, it is considered a climax species in harsh, rocky, and xeric sites (Veglen 1986, Rebertus et al. 1991, Donnegan & Rebertus 1999). Thus, the rapid decline and mortality seen during this study on both mesic and xeric sites implies that the observed decrease in the proportion of species composition that is limber pine, especially in subregions where increases in other species groups is absent, is not within typical forest succession patterns.

Regeneration

As seen in Smith et al. (2013), the short period in which small seedlings may become infected with WPBR, die, and degrade from a site makes determining trends in WPBR infection and mortality in regeneration difficult. Due to this, the WPBR incidence and mortality reported in this study may be underestimated. Additionally, our relatively long remeasurement periods (~5 years) make it difficult to determine what proportion of seedlings successfully grow into the 1.3 m height category and become integrated into the adult population. WPBR incidence in limber pine < 1.3 m decreased 1.4% from 5.3% in 2011-13 to 3.9% in 2016-17, however this change was not significant ($P = 0.4$), due to small sample size (39 stems overall). However, a significant change in WPBR mortality was observed over all plots combined, but not within separate subregions, likely also due to small sample size. WPBR mortality increased 1.6 ± 0.9% (*P* = 0.03) in limber pine < 1.3 m tall from 1.0% in 2011-13 to 2.6% in 2016-17 (Table 4). The highest WPBR incidence (11%) and mortality (4%) in regeneration was observed in Pole Mountain which followed trends of high rate of WPBR infections and mortality in this area for limber pine > 1.3 m tall.

Conversely, regeneration of all tree species was recorded robustly with a large sample size and allows insight into trends regarding density and species composition change over time. No significant changes in limber pine regeneration density were observed as there were 186 stems ha^{-1} in 2011-13 and 180 stems ha^{-1} in 2016-17 (*P* = 0.09) (Table 4). However, there was a significant increase in the species composition of limber pine (the proportion of regenerating species that is limber pine) in the Shoshone NF (+15%, *P* = 0.03) (Supplemental Table 14). This is interesting because though Shoshone NF lost a significant portion of limber pine > 1.3 m tall during the study, there is potential for increased regeneration to replenish the lost limber pine composition in this area. Additionally, a significantly higher density of limber pine regeneration was observed in Laramie Peak in 2011-13 (615 stem ha^{-1}) and 2016-17 (567 stems ha^{-1}) in comparison to other subregions (*P* = 0.03). This may imply recruitment in an area where a significant portion of limber pine > 1.3 m died during the study period (19%) and WPBR incidence is decreasing. In the Sangre de Cristo Mountains, significant decreases in density for trees < 1.3 m tall was observed for both limber (-2.2%, *P* = 0.01) and other pines (-6.9%, *P* = 0.01), including Rocky Mountain bristlecone (*P. aristata*) and ponderosa (*P. ponderosae*), while spruce-fir increased (+11.1% *P* = 0.01). As WPBR incidence increases in this region, continued monitoring will be needed to assess disease impacts in this area.

Correlation analyses for limber pine regeneration revealed weak to moderate associations between WPBR incidence and/or mortality to various stand and meteorological variables. Relative humidity in September had a moderately positive (R = 0.3, $P = 0.005$) association with WPBR incidence in 2011-13 and 2016-17 and WPBR mortality in 2016-17. Several other climatic variables had a weaker (R = 0.2, $P < 0.05$) relationship to WPBR incidence and mortality in regeneration such as water vapor pressure, growing season precipitation, precipitation in July and August, relative humidity in August, minimum and average temperatures in January and December. For WPBR mortality, few variables had significant relationships in both 2011-13 and 2016-17 (Supplemental Table 15), likely because of low sample sizes of WPBR-killed regeneration observed in this study. Significant p-values lend support to the validity of the relationships between these variables, however low R-values indicate the strength of those relationships is either moderate or weak.

Though all sites had a ≥ 20% composition of limber pine > 1.3 m, 34% of sites had no limber regeneration recorded during the 9-13 year study period; this occurred predominately in the Bighorn Mountains and Poudre South in 58% and 50% of sites, respectively. Additionally, 7% of sites had no regenerating species of any kind recorded during the study. Coupled with the significant decline and mortality of limber pine > 1.3 m tall, these numbers are unsettling regarding recruitment in these sites and the future of the limber pine in these areas.

Implications for management

As WPBR and episodic waves of MPB will continue to be prominent damage agents in these regions, long-term monitoring will be critical in preparing management plans for retaining and restoring this ecologically important species. Though there are inherent difficulties in maintaining long-term study plots in remote areas, the data provided by measuring monumented trees over time enables capture of large-scale and slow-progressing damages over time. Long-term surveys allow time series analysis and identification of subregions with high priority sites; which may be defined as having high (>50%) WPBR incidence or mortality (from WPBR or bark beetles), low density of limber pine, and/or low density of regeneration (Cleaver et al. 2015) for areas where limber pine is the sole species. Preservation of limber pine in these priority sites is important to maintaining the genetic diversity of the species, especially in regards to potentially WPBR-resistant trees. Additionally, management efforts to preserve multiple diameter classes within a designated priority site can promote stand resilience to both future bark beetle episodes and WPBR mortality (Schoettle & Sniezko 2007).

Conclusion

Due to the vast expanse and relatively slow growth of forest tree populations, long-term monitoring allows for evaluation of the effects of damage agents such as WPBR which can take years to kill the host. As WPBR is now a permanent biotic factor of the North American ecosystem, evaluating disease spread through the remaining range of white pines and the continued monitoring of intensification and impacts will be critical to developing appropriate management strategies to preserve these ecologically important species. Though it is apparent that MPB has returned to endemic levels, a large proportion of live limber pine that survived are classified as declining/dying, mostly due to WPBR and bark beetles. These results confirm that WPBR is negatively affecting the health of limber pine populations in the Rocky Mountains and will continue to do so over time. The dramatic increase in severity of WPBR infections, both at the tree and plot levels, is further evidence of this. The capture of the slow rate of WPBR's damaging effects is support for the value in installing and maintaining long-term survey plots to capture trends of these slow-acting, but devastating damage agents on our native tree populations.

CHAPTER 5: FUTURE DIRECTIONS

Long-term surveys allow for time series analysis of forest health conditions in order to identify and manage priority stands. The results of these studies enable management plans to target which sites have the highest impacts from specific biotic and/or abiotic factors. By identifying geographic regions and even individual stands as a priority for continued monitoring, restoration practices, and/or proactive management, resources can be utilized most efficiently towards promoting forest health. In areas with high WPBR and/or bark beetle mortality and low limber pine density and regeneration, it is likely that limber pine populations will be reduced. In highly impacted areas where limber pine is the sole tree species (harsh, xeric sites), restorative planting strategies should be considered to maintain the forested status of the site. Naturally occurring WPBR resistance is found in the limber pine population, both as a single gene (*Cr4)* conferring complete resistance and in the form of multi-gene resistance. Thus, identifying and protecting mature, resistant individuals from other damage agents (bark beetles, fire, etc.) and outplanting of resistant progeny into high impact areas may succeed in preserving limber pine as the climax species (Schoettle et al. 2014, Bingham 1972). As limber pine plays a dominant role in snowpack retention and erosion control on xeric, rocky sites, loss of trees on these sites will likely affect ecosystem function (Schoettle et al. 2004, Schoettle & Sniezko 2007). Additionally in healthy limber pine stands, a proactive management strategy should be applied in order to facilitate natural selection in favor of resistant individuals and promote stand resilience in order to reduce pest impacts in the future (Schoettle & Sniezko 2007).

Long-term studies provide specific information on various damage agents allowing for management strategies to be better suited to the needs of a particular stand. For example, seed collection, resistance screening, and outplanting of WPBR-resistant stock is a viable option for proactive management of limber pine stands likely to be impacted by WPBR in the future (Schoettle and Sniezko 2007). Additionally, limber pine already on-site with complete or partial resistance to WPBR should be protected against other damage agents such as bark beetles, dwarf mistletoe, and fire. During the most recent MPB epidemic, the use of the anti-aggregation pheromone, verbenone, on highly-valued limber pines with known resistance likely protected the natural gene pool of WPBR-resistance (Schoettle et al. 2011), however it is unknown how many WPBR-resistant trees may have been lost to beetles during the epidemic. Lastly, proactive management to maintain multiple age and diameter classes within a stand can provide resilience against the diameter preferences of bark beetles and high mortality in smaller diameter trees due to WPBR (Schoettle and Sniezko 2007). The use of long-term monitoring studies allows these specific management strategies to be applied to regions most impacted by specific damage agents. Currently, long-term monitoring sites are being established in Montana (Jackson et al. 2010), and in addition to the sites measured within this study, provide a large portion of the U.S. Rocky Mountains under continued survey. Additional sites would be necessary in southern Colorado and New Mexico in order to encompass the entirety of limber pine's range in the U.S.

Though there are inherent difficulties in installing, maintaining, and re-measuring limber pine sites, as they often grow in remote, rocky areas, the results gained from time series analysis of long-term data are invaluable for capturing trends in a forest landscape. As limber pine can live over 1,000 years and take up to 50 years to reach maturity, the 10 year span of this survey is just a snapshot of what damages these trees may encounter (Steele 1990, Schoettle 2004). Further, the amount of decline and death witnessed during this relatively short survey period is remarkable and further warrants the upkeep and continued monitoring of these sites. It is known that damages caused by pathogens (WPBR) and insects (MPB/*Ips*) can occur in waves (Gibson et al. 2008, Kinloch 2003), thus the addition of more time points to these already established sites can not only capture the peaks of these waves, but also the lulls to establish a baseline of limber pine health trends. Additionally, as climate change modeling predicts that WPBR and MPB/Ips occurrence may increase in the future, these long-term studies will be critical for analyzing whether episodic waves are increasing in frequency and/or intensity (Kipfmueller et al. 2002, Larson 2011). Unfortunately, the measurement period (5 years) and site placements (few stems < 1.3 m) of this study were too course to capture regeneration metrics efficiently. Possible solutions to this may include shortening the remeasurement period, which has the added benefit of increasing the data points in the time series analysis.

Management efforts should focus on areas identified in this long-term study with high WPBR and mortality and low limber pine density and regeneration, such as Pole Mountain, Shoshone NF, Montana, and Canyon Lakes for preservation and/or restoration efforts in stands where limber pine is the sole species. Healthier, but still declining subregions, such as the Bighorn Mountains, Laramie Peak, Poudre South and Sangre de Cristo Mountains should be considered for continued monitoring and possibly proactive management strategies. The Sangre de Cristo Mountains especially, that lie near the current WPBR disease front, should be considered for future monitoring as increasing incidence rates here may hint at the potential for the large health decline and mortality seen in regions further north. As severity was not measured in Sangre de Cristo limber pine previously, continued monitoring will be critical in this region to see how current WPBR infections are impacting these high-elevation white pines and how new infections and mortality may occur in the future. Additionally, none of our long-term sites lie between Rocky Mountain National Park in northern Colorado and the Wet and Sangre de Cristo

Mountains in southern Colorado, thus more long-term sites in central Colorado would be necessary to effectively monitor white pines in this high-elevation area.

Throughout most of the Rocky Mountains, limber pines are declining or dying at a substantial rate. Though WPBR is a devastating damage agent and is now a permanent member of the North American forest ecosystem, it is unlikely that this biotic agent alone will eliminate limber pine in the U.S. However, a large portion of the limber pine population encompassed in this survey have been severely affected by the combined effects of WPBR and bark beetles. The recent MPB epidemic has subsided but will likely continue to occur in the future. Additionally, studies suggest that changing climates will reduce suitable environments for limber pine (Monahan et al. 2013) and limber pine basal areas will be reduced 44% by 2027 (Krist et al. 2014). These combining risk factors make the future of limber pine in the U.S. Rocky Mountains uncertain. With this knowledge, it is suggested that federal protective status be applied to limber pine in the U.S. similar to Canada where the Species at Risk Act (2002) has promoted limber pine to endangered status. Additionally, financial resources will be necessary to fund future monitoring and management plans to observe changes in limber pine health, manage stands appropriately, and preserve mature trees and promote regeneration of this ecologically important species.

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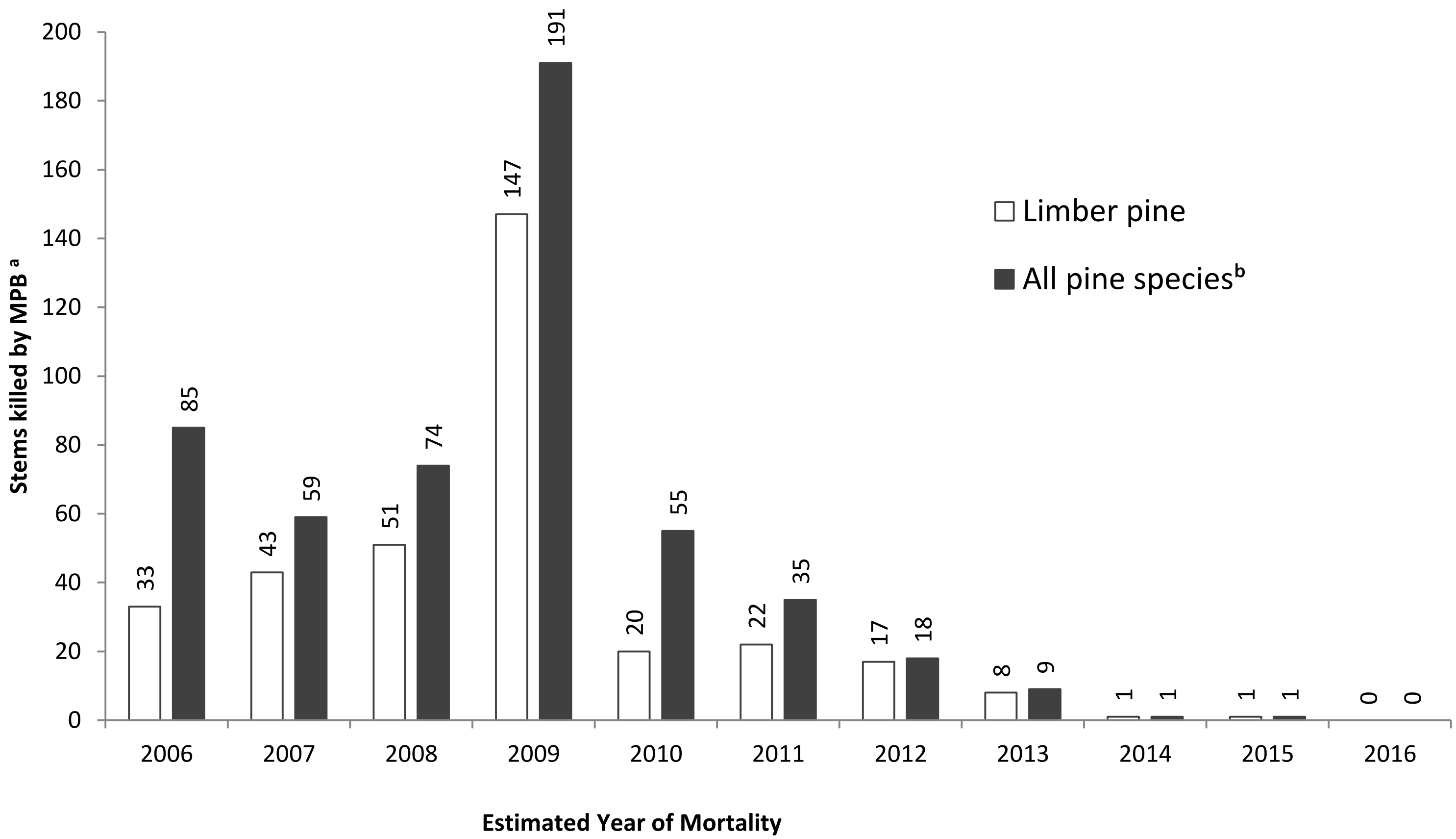
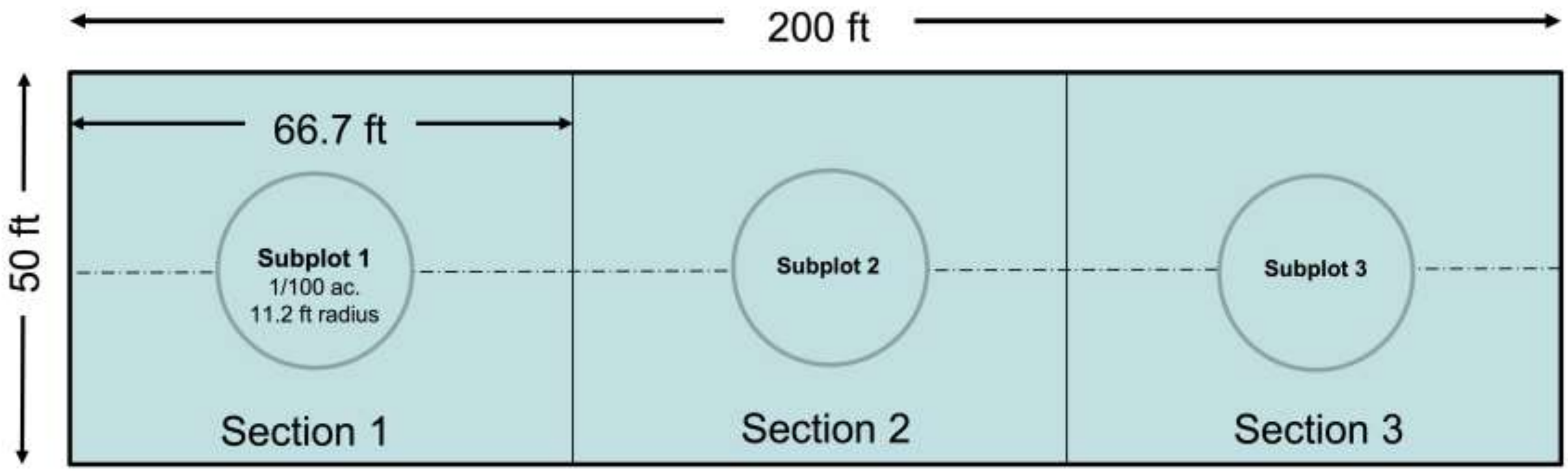
APPENDIX: SUPPLEMENTAL FIGURES AND TABLES



Supplemental Figure 1 – MPB/Ips Mortality by Estimated Year of Death for Trees > 1.3 m tall – (a) Stems killed by MPB or *Ips* spp. were estimated for year of death by assessing the condition of fine twigs, small branches, and bark degradation over time (see Methods); (b) All pine species includes: Limber pine (*Pinus flexilis*), whitebark pine (*P. albicaulis*), lodgepole pine (*P. contorta* subsp. *latifolia*), and ponderosa pine (*P. ponderosae*).



Supplemental Figure 2 – Plot Layout – To scale schematic of plot layout for sites in COWY, NOWY, MT and ND. In SOCO (Sangre de Cristo Mountains) plot layout was similar but with length and width adjusted to include ~30 white pines per site. On average, SOCO plots were 200’x50’ whereas sites elsewhere were standardized to 200’x50’.

Supplemental Table 1 - Meteorological Variables[a] used in Pearson correlation analysis to WPBR incidence and mortality[b]

Moderate or greater drought frequency: 12, 36, and 60 month
Frost free period: Frost free days (# days), length frost free period (# days)
Julian date of last freezing date of spring
Julian date of first freezing date of autumn
Growing degree days
Standardized moisture difference z-score
Growing season precipitations (mm)
Annual moisture index: ratio of degree days > 5°C to annual precipitation (mm)
Mean annual precipitation
Mean precipitation for each month (mm)
Mean May-June and July – September precipitation (mm)
Ratio growing season precipitation : mean annual precipitation
Seasonal moisture index: ratio of degree-days > 5°C accumulating within the frost-free period to seasonal precipitation
Short wave radiation (direct, diffuse, and derived)
Average temperature & average min. temperature in coldest month (tenths degree C)
Average minimum temperature each month
Average minimum temperature May - June & July - September
Average temperature & average maximum temperature for warmest month (tenths degree C)
Average temperature & average maximum temperature for year overall and each month
Average temperature & average maximum temperature May – June & July – September
Water vapor pressure
Annual average relative humidity
Average relative humidity each month
Average relative humidity May – June & July – September
Growing season precipitation (mm)
Annual precipitation (mm)
Mean annual temperature – tenths of degree Celsius
1st principal component: average temperature, monthly precipitation, minimum & maximum temperatures
2nd principal component: minimum temperature, monthly precipitation
Ratio of growing season precipitation to annual precipitation
Soil component dominance & frequency
Julian date when sum of degree-days > 5°C reaches 100
Degree-days < 0°C
Degree-days >5°C
Soil drainage index – derived from SSURGO/STATSGO/NFS
Soil data source - SSURGO/STATSGO/NFS
Fertility index - SSURGO/STATSGO/NF
Growing-degree days
Degree days >5°C accumulating within frost free period
Topographic Relative Moisture Index (and modified)
Topographic scale
Wind variability, strength, & direction: Monthly, yearly, and seasonally (May - June and Sept - Oct)

[a]Variables acquired from Cleaver et al. (2015)
[b]Data obtained through FHAAST (USDA Forest Health Assessment and Applied Sciences Team, Fort Collins, CO) via PRISM dataset and Daymet Daily Surface Gridded Data (1km grid). Data obtained as averages over years 1985 – 2016

Supplemental Table 2 - Plot level variables used in Pearson/Spearman correlations (28 x 137 variables)[a]

WPBR Incidence 2004-07, 2011-13, 2016-17	Percent of 'Spruce-Fir' declining/dying 2004-07	WPBR Incidence limber each dbh class in 2004-07	WPBR Incidence Regeneration (<1.3m) 2011-13
Percent of 'Other Pine' declining/dying 2016-17	WPBR mortality with bark beetle damage 2016-17	WPBR Incidence limber each dbh class in 2011-13	WPBR Incidence Regeneration (<1.3m) 2016-17
Percent of 'Other Pine' declining/dying 2004-07	WPBR mortality with bark beetle damage 2011-13	WPBR Incidence limber each dbh class in 2016-17	WPBR Mortality Regeneration (<1.3m) 2011-13
Percent of 'Spruce-Fir' declining/dying 2016-17	WPBR Mortality 2004-07, 2011-13, 2016-17		WPBR Mortality Regeneration (<1.3m) 2016-17
Elevation	Density Live Limber (stems/ha) 2016-17	Average temperature in coldest month	Julian date of the first freezing date of autumn
Bearing	Basal Area all spp. (m^2/ha) 2016-17	Average temperature in warmest month	Length of the frost-free period
Slope	Basal Area all spp. (ft^2/acre) 2016-17	Growing degree days	12 month moderate or greater drought frequency
Aspect	Basal Area Live Limber (m^2/ha) 2016-17	Degree days >5 °C within the frost-free period	36 month moderate or greater drought frequency
Latitude	Basal Area Live Limber (ft^2/acre) 2016-17	Landform	60 month moderate or greater drought frequency
Longitude	Density all spp. (stem/ha) 2011-13	Land cover – NLCD 2002	Autumn frost date
Number living limber <5 cm tall (2016-17)	Density All Limber (stems/ha) 2011-13	Minimum degree days <0 °C	Spring frost date
Number living limber 5.1-15.2 cm tall (2016-17)	Percent of total density that is limber (2011-13)	Julian date of the last freezing date of spring	Frost free period
Number living limber 15.3-30.5 cm tall (2016-17)	Density Live Limber (stems/ha) 2011-13	Topographic relative moisture index	Growing degree days
Number living limber >30.5 cm tall (2016-17)	Basal Area all spp. (m^2/ha) 2011-13	Topographic scale	USDA plant hardiness zone
Number living limber <5 cm tall (2011-13)	Basal Area all spp. (ft^2/acre) 2011-13	Seasonal moisture index – ratio of degree days to seasonal precipitation	Growing season precipitation
Number living limber 5.1-15.2 cm tall (2011-13)	Basal Area Live Limber (m^2/ha) 2011-13	Ratio of growing season precipitation (ppt) to annual ppt	Annual moisture index: ratio of degree-days >5°C to annual ppt
Number living limber 15.3-30.5 cm tall (2011-13)	Basal Area Live Limber (ft^2/acre) 2011-13	Direst short-wave radiation	Mean annual precipitation
Number living limber >30.5 cm tall (2011-13)	Density all spp. (stem/ha) 2004-07	Diffuse short-wave radiation	Precipitation for each of 12 months separately
Number living limber <5 cm tall (2004-07)	Density All Limber (stems/ha) 2004-07	Slope (0.5% integer scale)	Ratio growing season precipitation to mean annual precipitation
Number living limber 5.1-15.2 cm tall (2004-07)	Percent of total density that is limber (2004-07)	Derived short-wave radiation	Seasonal moisture index – ratio of growing season degree-days >5°C to seasonal precipitation
Number living limber 15.3-30.5 cm tall (2004-07)	Density Live Limber (stems/ha) 2004-07	Short-wave radiation	Average temperature coldest month
Number living limber >30.5 cm tall (2004-07)	Basal Area all spp. (m^2/ha) 2004-07	1st Principle component - average temperature	Average minimum temperature coldest month

Percent of site that is 'Other Pines' (2016-17)	Basal Area all spp. (ft^2/acre) 2004-07	1st Principle component – maximum temperature	Average minimum temperature for each of 12 months separately
Percent of site that is 'Spruce-Fir' (2016-17)	Basal Area Live Limber (m^2/ha) 2004-07	1st Principle component – minimum temperature	Average maximum temperature warmest month
Percent of site that is 'Other Spp.' (2016-17)	Basal Area Live Limber (ft^2/acre) 2004-07	2nd Principle component – minimum temperature	Average maximum temperature for year
Percent of cankers in lower third 2011-13	Percent of Basal Area that is Limber 2004-07	Water vapor pressure	Average maximum temperature for each of 12 months separately
Percent of cankers in lower third 2016-17	Canopy Cover	Annual moisture index	Average temperature warmest month
Percent of cankers in middle third 2011-13	Curvature arc – from Digital Elevation Model	Soil component dominance	Average temperature for year (mean annual temperature)
Percent of cankers in middle third 2016-17	Digital Elevation Model – NED 30m	Soile component frequency	Average temperature for each of 12 months separately
Percent of cankers in upper third 2011-13	Slope * cos(aspect) – NED 30m	Julian date when sum of degree-days >5°C reaches 100	Water vapor pressure
Percent of cankers in upper third 2016-17	Growing season precipitation (mm)	Degree-days <0°C	Annual average relative humidity
Density all spp. (stem/ha) 2016-17	Impervious surface – NLCD 2002	Degree-days >5°C	Monthly average relative humidity for each month
Density All Limber (stems/ha) 2016-17	Annual precipitation (mm)	Soil drainage index – SSURGO/STATSGO/NFS	Basal area (sqft/acre) of limber pine
Percent of total density that is limber 2016-17	Mean annual temperature	Soil data source - SSURGO/STATSGO/NFS	Percent of total basal area that is limber pine
Slope * sin(aspect) – NED 30 m	Maximum temperature in warmest month	Ecomap sub-section id	Total trees per acre (all spp.)
Slope position index – NLCD NED 30 m	Minimum temperature in coldest month	Number of frost-free days	Total basal area (all species, sqft/acre)
Fertility index - SSURGO/STATSGO/NFS			

[a] 26 variables in top table were used in Pearson or Spearman correlation analysis against 137 variables in lower table

Supplemental Table 3 – Subplot level variables used in Pearson/Spearman correlations (5 x 18 variables)[a]

WPBR Incidence 2004-07
WPBR Incidence 2011-13
WPBR Incidence 2016-17
WPBR Mortality 2011-13
WPBR Mortality 2016-17

Proportion that is soil 2004-07
Proportion that is litter 2004-07
Proportion that is vegetation 2004-07
Proportion that is lichen/moss 2004-07
Proportion that is trees/logs 2004-07
Proportion that is rock 2004-07
Proportion that is soil 2011-13
Proportion that is litter 2011-13
Proportion that is vegetation 2011-13
Proportion that is lichen/moss 2011-13
Proportion that is trees/logs 2011-13
Proportion that is rock 2011-13
Proportion that is soil 2016-17
Proportion that is litter 2016-17
Proportion that is vegetation 2016-17
Proportion that is lichen/moss 2016-17
Proportion that is trees/logs 2016-17
Proportion that is rock 2016-17

[a] 5 variables in top table were used in Pearson or Spearman correlation analysis against 18 variables in lower table

Supplemental Table 4 – Variables from WPBR-infected tree measurements used in Pearson/Spearman correlations (6 x 20 variables)[a]

Diameter at breast height 2004-07
Diameter at breast height 2011-13
Diameter at breast height 2016-17
Percent of crown killed 2004-07
Percent of crown killed 2011-13
Percent of crown killed 2016-17

Health Status in 2004-07
Health Status in 2011-13
Health Status in 2016-17
Total number cankers 2004-07
Total number cankers 2011-13
Total number cankers 2016-17
Number of stem cankers 2011-13
Number of stem cankers 2016-17
Number of stem cankers in lower third 2011-13
Number of stem cankers in lower third 2016-17
Number of cankers in lower third 2011-13
Number of cankers in middle third 2011-13
Number of cankers in upper third 2011-13
Number of cankers in lower third 2016-17
Number of cankers in middle third 2016-17
Number of cankers in upper third 2016-17
Total number branch cankers 2011-13
Total number branch cankers 2016-17
Six & Newcombe severity 2011-13
Six & Newcombe severity 2016-17

[a] Six variables in top table were used in Pearson/Spearman correlation analysis against 20 variables in lower table. All values used in analysis were collected from live, infected limber pine.

Supplemental Table 5 – Species Composition of Sites for Trees > 1.3 m tall

Study Area		# Stems - all species Live (Total)		# Stems per Group – Live (Total) (Live Percent of # Stems - all species)[a]							
				Limber Pine		**Other Pine[b]**		**Spruce-Fir[c]**		**Other spp.[d]**	
		04-07	**16-17**	**04-07**	**16-17**	**04-07**	**16-17**	**04-07**	**16-17**	**04-07**	**16-17**
Overall		**6952** (7247)	**6479** (8206)	**3625** (3870) **(53.4)**	**3115** (4176) **(44.8)**	891 (909) (14.4)	732 (1024) (13.1)	**1081** (1097) **(17.3)**	**1174** (1311) **(21.1)**	**1085** (1101) **(17.4)**	**1167** (1397) **(21.0)**
SOCO	Sangre de Cristo Mtns	**417** **(422)**	**542** **(639)**	**150** (150) **(35.2)**	**201** (229) **(37.6)**	107 (107) (22.7)	157 (179) (29.4)	**102 (103)** **(26.6)**	**131 (148)** **(23.6)**	**58** (59) **(15.5)**	**49** (79) **(8.7)**
COWY	Canyon Lakes	715 **(729)**	654 **(876)**	223 **(237)** (31.2)	195 **(263)** (29.8)	**358 (358)** **(49.1)**	**275 (401)** **(42.0)**	80 **(80)** (11.0)	74 **(88)** (11.3)	54 (54) (7.4)	110 (124) (16.8)
	Laramie Pk	755 **(784)**	673 **(915)**	335 **(363)** (44.4)	308 **(402)** (45.8)	148 (148) (18.9)	131 (167) (19.5)	172 (172) (21.9)	129 (199) (19.2)	100 (101) (12.9)	105 (147) (15.6)
	Pole Mtn	**741** **(743)**	**530** **(804)**	**311** (311) **(41.9)**	**204** (327) **(38.5)**	227 (228) (30.7)	172 (260) (32.5)	42 (42) (5.7)	42 (42) (7.9)	161 (162) (21.8)	112 (175) (21.1)
	Snowy Mtns	340 **(348)**	349 **(417)**	231 **(238)** (67.9)	209 **(261)** (59.9)	20 (21) (6.0)	16 (21) (4.6)	60 (60) (17.2)	90 (91) (25.8)	29 (29) (8.3)	34 (44) (9.7)
	Poudre South	336 (348)	360 (417)	225 (237) (66.9)	211 (255) (58.6)	29 (29) (8.3)	26 (31) (7.2)	57 (57) (16.4)	61 (63) (16.9)	25 (25) (7.2)	62 (68) (17.2)
NOWY	Shoshone	802 (897)	714 (1029)	**546 (633)** **(68.1)**	**390 (670)** **(54.6)**	4 (4) (0.4)	4 (4) (0.6)	132 **(134)** (14.9)	130 **(143)** (18.2)	120 (126) (14.0)	190 (212) (26.6)
	Bighorn	790 **(844)**	835 **(956)**	395 (420) (50.0)	377 (458) (45.1)	77 (88) (10.4)	88 (104) (10.5)	**138 (148)** **(17.5)**	**192 (206)** **(23.0)**	180 (188) (22.3)	178 (188) (21.3)
MT		1324 **(1379)**	1228 **(1541)**	**610 (656)** **(46.1)**	**507 (718)** **(41.3)**	28 (33) (2.4)	20 (36) (1.6)	400 **(404)** (29.3)	456 **(479)** (37.1)	285 **(285)** (20.7)	245 **(308)** (20.0)
ND		225 (251)	225 (251)	94 (120) (41.8)	94 (120) (41.8)	0 (0) (0)	0 (0) (0)	0 (0) (0)	0 (0) (0)	131 (131) (58.2)	131 (131) (58.2)

[a] Number live stems per group divided by number live stems for all species
[b] Other pine includes: *Pinus contorta* subsp. *latifolia*, *P. ponderosae*, *P. albicaulis*, *P. aristata*.
[c] Spruce-Fir includes: *Pseudotsuga menziesii*, *Abies lasiocarpa*, *A. concolor*, *Picea engelmannii.*
[d] Other spp. includes: *Juniperus scopulorum*, *Populus tremuloides*
Bolded values indicate significant change (p < 0.05) using McNemar's test from 2004-07 to 2016-17 within subregion

Supplemental Table 6 – Proportion of Live Limber Pine (> 1.3 m tall) across Diameter Classes

Study Area[a]		# Live Stems		# Stems in diameter class [b] (% of Live Stems)											
				<5cm DBH			5.1-15.2cm			15.3-30.5cm			>30.5cm		
		04-07	16-17	04-07	16-17	Change (%)	04-07	16-17	Change (%)	04-07	16-17	Change (%)	04-07	16-17	Change (%)
Overall		**3625**	**3115**	**1009 (27.8)**	**843 (27.1)**	**-16.5**	**1412 (39.0)**	**1268 (40.7)**	**-10.2**	**958 (26.4)**	**795 (25.5)**	**-17.0**	246 (6.8)	207 (6.6)	-15.9
SOCO	Sangre de Cristo Mtns	**655**	**620**	**158 (24.1)**	**126 (20.3)**	**-20.3**	215 (32.8)	207 (33.4)	-3.7	189 (28.9)	184 (29.7)	-2.6	**93 (14.2)**	**103 (16.6)**	**+10.8**
COWY	Canyon Lakes	**223**	**195**	94 (42.2)	76 (39.0)	-19.1	95 (42.6)	88 (45.1)	-7.4	31 (13.9)	29 (14.9)	-6.4	3 (1.3)	2 (1.0)	-33.3
	Laramie Pk	**335**	**308**	172 (51.3)	155 (50.3)	-9.9	116 (34.6)	115 (37.3)	-0.9	43 (12.8)	34 (11.0)	-20.9	4 (1.2)	4 (1.3)	0
	Pole Mtn	**311**	**204**	**110 (35.4)**	**51 (25.1)**	**-53.6**	**147 (47.3)**	**116 (57.1)**	**-21.1**	48 (15.4)	34 (16.7)	-29.2	6 (1.9)	2 (1.0)	-66.7
	Snowy Mtns	231	209	38 (16.5)	43 (20.6)	+13.1	**108 (46.8)**	**92 (44.0)**	**-14.8**	66 (28.6)	58 (27.8)	-12.1	19 (8.2)	16 (7.7)	-15.8
	Poudre South	225	211	49 (21.8)	50 (23.8)	+2.0	79 (35.1)	80 (38.1)	+1.2	87 (38.7)	73 (34.8)	-16.1	10 (4.4)	7 (3.3)	-30.0
NOWY	Shoshone	**546**	**390**	125 (22.9)	97 (24.9)	-22.4	**208 (38.1)**	**172 (44.1)**	**-17.3**	**170 (31.1)**	**98 (25.1)**	**-42.4**	43 (7.9)	23 (5.9)	-46.5
	Bighorn	**395**	**377**	61 (15.4)	72 (19.1)	+18.0	140 (35.4)	127 (33.7)	-9.3	149 (37.7)	138 (36.6)	-7.4	45 (11.4)	40 (10.6)	-11.1
MT		**610**	**507**	173 (28.4)	144 (28.4)	-16.8	255 (41.8)	222 (43.8)	-12.9	159 (26.1)	131 (25.8)	-17.6	23 (3.8)	10 (2.0)	-56.5
ND		94	94	29 (30.9)	29 (30.9)	0	49 (52.1)	49 (52.1)	0	16 (17.0)	16 (17.0)	0	0 (0)	0 (0)	0

[a] SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota.

[b] Change reflects the decrease in live stems per diameter class divided by stems in that class in 2004-07.

Bolded values indicate significant change ($p < 0.05$) using McNemar's test from 2004-07 to 2016-17 within subregion

Supplemental Table 7 - Change in Limber (> 1.3 m tall) Health Status (2004-07 to 2016-17)

Study Area [a]		Total limber stems >1.3m [b]	Number of Stems >1.3m (% of total)			
			Stable as Healthy [c]	Health Improved [d]	Health Declined [e]	Died during Study [f]
Overall		3701	2032 (54.9)	68 (1.8)	**822 (22.2)**	**779 (21.1)**
SOCO	Sangre de Cristo Mtns	664	456 (68.7)	0 (0)	**135 (20.3)**	**73 (11.0)**
COWY	Canyon Lakes	233	109 (46.8)	1 (0.4)	**71 (30.5)**	**52 (22.3)**
	Laramie Pk	351	226 (64.4)	3 (0.8)	56 (16.0)	**66 (18.8)**
	Pole Mtn	311	119 (38.3)	2 (0.6)	72 (23.2)	**118 (37.9)**
	Snowy Mtns	237	145 (61.2)	1 (0.4)	**60 (25.3)**	**31 (13.1)**
	Poudre South	225	143 (63.6)	1 (0.4)	52 (23.1)	29 (12.9)
NOWY	Shoshone	561	222 (39.5)	2 (0.4)	**148 (26.4)**	**189 (33.7)**
	Bighorn	397	239 (60.2)	0 (0)	**96 (24.2)**	62 (15.6)
MT		628	279 (44.5)	58 (9.2)	**132 (21.0)**	**159 (25.3)**
ND		94	94 (100)	0 (0)	0 (0)	0 (0)

[a] SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota.
[b] Includes all trees (live and dead) but does not include trees classified as old dead or <1.3m tall in 2004-07.
[c] Health status of 1 (<15% damage to crown/stem) throughout survey period.
[d] Health status was greater than 1 (>16% damage to crown/stem) but reduced to a healthy status by end of survey period.
[e] Damage accrued in the crown/stem throughout study period, trees in this category began as health status 1 and declined to status 2 (16-50% damage) or status 3 (>50% damage).
[f] Trees that were alive at beginning of survey but died within the study period from any cause.
Bolded values indicate significant change ($p < 0.05$) using McNema'rs test from 2004-07 to 2016-17 within subregion

Supplemental Table 8 –Mortality of Limber Pine (>1.3m tall)

Study Area		# Dead stems recorded		Cause of Mortality (% of dead stems)											
				MPB/*Ips* spp. [a]			WPBR + Bark Beetles[b]	WPBR[c]	Other + WPBR[d]			Other			
		04-07	16-17	04-07	16-17	Change ±SE	16-17	16-17	04-07	16-17	Change ±SE	04-07	16-17	Change ±SE
Overall		245	1015	**0.9**	**8.4**	**7.5±0.8**	3.4	2.8	**0.5**	**2.5**	**2.0±0.6**	**5.0**	**9.2**	**4.2±0.5**
SOCO	Sangre de Cristo Mtns	0	74	0	0	--	0	2.1	0.2	0.3	--	0.3	8.1	--
COWY	Canyon Lakes	14	59	**0**	**8.9**	**8.9±0.1**	1.1	2.3	0	0.8	0.8±1.4	5.9	9.9	4.0±2.0
	Laramie Pk	28	94	0.6	3.2	2.7±1.5	2.7	3.2	0.3	0.7	0.5±1.1	6.9	13.7	6.8±3.9
	Pole Mtn	0	119	0	1.6	--	12.0	13.5	0	7.4	--	0	2.1	--
	Snowy Mtns	7	39	**2.5**	**13.0**	**10.5±2.0**	1.1	0	0	0	0	0.4	1.5	1.1±0.9
	Poudre South	12	40	0.4	9.0	8.6±2.2	2.4	0	0	0	0	4.6	7.1	2.4±0.6
NOWY	Shoshone	87	277	**2.1**	**15.0**	**13.0±3.5**	6.3	3.1	0	1.8	1.8±0.7	**11.7**	**15.5**	**3.8±0.7**
	Bighorn	25	82	0.5	6.9	6.5±1.7	3.7	0.7	0	1.3	1.3±2.6	5.5	5.7	0.2±0.2
MT		46	205	1.7	8.3	6.6±1.2	2.8	2.0	2.6	7.6	5.0±1.3	**2.8**	**8.6**	**5.8±1.1**
ND															

[a] Majority of damage causing death from MPB or *Ips* beetles.
[b] Equal damages from WPBR infection and bark beetles (especially MPB) resulted in death.
[c] Trees classified as old dead in 2004-07 were not measured for WPBR infection.
[d] Trees killed by damages from other causes, but had WPBR infection contributing to health decline.
Bolded values indicate significant change ($p < 0.05$) using McNemar's test from 2004-07 to 2016-17 within subregion

Supplemental Table 9 – WPBR Infection in Limber Pine Killed by Mountain Pine Beetle/Ips Beetles

Study Area		Limber Pine (>1.3m tall) killed by MPB/Ips in sites w/ >20% WPBR Incidence	# Killed by MPB/Ips (% of total)	
			Infected w/ WPBR	Uninfected
Overall		153	87 (56.9)	66 (43.1)
SOCO	Sangre de Cristo Mtns	0	0 (0)	0 (0)
COWY	Canyon Lakes	1	0 (0)	1 (100)
	Laramie Pk	4	3 (75.0)	1 (25.0)
	Pole Mtn	26	21 (80.8)	5 (19.2)
	Snowy Mtns	4	1 (25.0)	3 (75.0)
	Poudre South	0	0 (0)	0 (0)
NOWY	Shoshone	38	29 (76.3)	9 (23.7)
	Bighorn	49	17 (34.7)	32 (65.3)
MT		31	16 (51.6)	15 (48.4)
ND		0	0 (0)	0 (0)

SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota

Supplemental Table 10 – WPBR and Bark Beetle (BB)[a] Mortality in Limber Pine (> 1.3 m tall) across Diameter Classes

Study Area[b]		# Stems Killed[c]		Mortality by Diameter Class (% of stems killed)							
				<5cm DBH		5.1-15.2cm		15.3-30.5cm		>30.5cm	
		WPBR	BB	WPBR	BB	WPBR	BB	WPBR	BB	WPBR	BB
Overall		159	272	47.2	4.0	44.7	21.7	6.3	56.3	1.9	18.0
SOCO	Sangre de Cristo Mtns	15	0	53.3	0	46.7	0	0	0	0	0
COWY	Canyon Lakes	8	22	75.0	9.1	25.0	31.8	0	50.0	0	9.1
	Laramie Pk	20	12	15.0	16.7	75.0	41.7	10.0	33.3	0	8.3
	Pole Mtn	62	5	56.5	20.0	37.1	40.0	4.8	40.0	1.6	0
	Snowy Mtns	0	32	0	3.1	0	25.0	0	65.6	0	6.3
	Poudre South	0	16	0	0	0	0	0	68.8	0	31.3
NOWY	Shoshone	28	98	28.6	3.1	60.7	18.4	10.7	61.2	0	17.3
	Bighorn	6	30	50.0	3.3	16.7	13.3	16.7	46.7	16.7	36.7
MT		20	56	60.0	1.8	30.0	25.0	5.0	53.6	5.0	19.6
ND		0	1	0	0	0	100	0	0	0	0

[a] Bark beetles include mountain pine beetle and/or *Ips* spp.
[b] SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota
[c] Total number of limber pine stems killed by WPBR or MPB/Ips – trees where both WPBR and MPB/Ips contributed to mortality excluded.

Supplemental Table 11 – WPBR Incidence in Limber Pine (> 1.3 m tall) across Diameter Classes

Study Area[a]		# Live Infected Stems		Incidence[b] % of total infected (# stems infected)							
				<5cm DBH		5.1-15.2cm		15.3-30.5cm		>30.5cm	
		2004-07	2016-17	04-07	16-17	04-07	16-17	04-07	16-17	04-07	16-17
Overall		**1070**	**809**	**20.3 (214)**	**14.2 (127)**	**46.2 (481)**	**44.0 (406)**	28.3 (293)	33.2 (309)	5.2 (64)	8.6 (80)
SOCO	Sangre de Cristo Mtns	**59**	**128**	16.9 (10)	14.4 (15)	52.5 (31)	41.4 (54)	**22.0 (13)**	**26.5 (37)**	**8.5 (5)**	**17.7 (25)**
COWY	Canyon Lakes	52	35	32.7 (17)	16.7 (8)	61.5 (32)	62.5 (30)	5.8 (3)	20.8 (10)	0 (0)	0 (0)
	Laramie Pk	71	49	22.5 (16)	20.3 (12)	57.7 (41)	55.9 (33)	18.3 (13)	22.0 (13)	1.4 (1)	1.7 (1)
	Pole Mtn	**202**	**104**	**28.7 (58)**	**13.9 (15)**	**48.0 (97)**	**59.3 (64)**	21.3 (43)	25.9 (28)	2.0 (4)	0.9 (1)
	Snowy Mtns	**38**	**42**	5.3 (2)	8.5 (4)	31.6 (12)	19.1 (9)	**42.1 (16)**	**51.1 (24)**	21.1 (8)	21.3 (10)
	Poudre South	1	1	0 (0)	0 (0)	0 (0)	0 (0)	100 (1)	100 (1)	0 (0)	0 (0)
NOWY	Shoshone	170	111	14.7 (25)	7.1 (9)	45.9 (78)	48.4 (61)	31.2 (53)	33.3 (42)	8.2 (14)	11.1 (14)
	Bighorn	145	128	7.6 (11)	11.3 (16)	**33.8 (49)**	**28.2 (40)**	44.1 (64)	44.4 (63)	14.5 (21)	16.2 (23)
MT		**332**	**211**	23.9 (75)	18.5 (48)	**44.8 (141)**	**44.2 (115)**	27.7 (87)	35.0 (91)	3.6 (11)	2.3 (6)

[a] SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana, ND: North Dakota

[b] The number of live, infected limber >1.3m tall divided by total number of live limber >1.3m tall

Bolded values indicate significant change ($p < 0.05$) using paired T-test within subregion on count data

Supplemental Table 12 – White Pine Blister Rust Canker Assessment[a]

Study Area[b]		Total # cankers measured (# stem cankers[c])			# Cankers per tree (mean ± SE)			# Trees with 1+ stem canker in lower 1/3 (% of total infected[e])		
		04-07	**11-13**	**16-17**	**04-07**	**16-17**	**Change ±SE**	**11-13**	**16-17**	**Change**
Overall		2150	2451[d] (548)	2714 (818)	3.7	3.3	-0.4±0.1	**83 (13.4)**	**144 (17.6)**	**+4.2%**
SOCO	Sangre de Cristo Mtns	88 (12)	--	392 (97)	2.3	3.0	0.7±0.1	--	26 (20.0)	--
COWY	Canyon Lakes	88	150 (55)	130 (62)	2.8	3.2	0.4±0.1	7 (20.6)	9 (22.0)	+1.4%
	Laramie Pk	50	133 (53)	103 (52)	**1.5**	**2.1**	**0.6±0.2**	7 (18.9)	11 (22.9)	+4.0%
	Pole Mtn	393	515 (65)	445 (107)	4.2	4.2	0±0.1	13 (13.3)	25 (23.8)	+10.5%
	Snowy Mtns	75	98 (12)	98 (18)	2.7	2.8	0.1±0.2	2 (6.1)	8 (19.0)	+13.0%
	Poudre South	2	2 (0)	2 (0)	2.0	2.0	0±0.1	0 (0)	0 (0)	+0%
NOWY	Shoshone	403	339 (74)	400 (105)	4.7	3.6	-1.1±0.1	9 (9.1)	16 (14.3)	+5.2%
	Bighorn	589	667 (98)	587 (120)	5.8	4.6	-1.2±0.3	**15 (12.5)**	**26 (20.5)**	**+8.0%**
MT		462	547 (179)	537 (257)	2.8	2.5	-0.3±0.1	30 (15.2)	49 (23.2)	+8.0%

[a] Cankers were determined either by presence of aecia/pycnia or three of the five WPBR indicators (see Methods).
[b] No cankers were present in ND. SOCO: southern Colorado, COWY: northern Colorado/southern Wyoming, NOWY: northern Wyoming, MT: Montana.
[c] Stem cankers were differentiated from total cankers in 2011-13 measurements onward.
[d] Overall value does not include SOCO data in 2011-13.
[e] Data regarding crown thirds was recorded in 2011-13 and 2016-17. Percent of total infected was calculated as number of trees with a stem canker in lower crown 1/3 divided by number of live infected trees.
Bolded values indicate significant change ($p < 0.05$) using McNemar's test (count data) or paired T-test (means) within subregion

Supplemental Table 13 – Significant[a] correlations in Limber Pine (> 1.3 m tall) to WPBR incidence/mortality

Significant variables in incidence correlations	WPBR Incidence: Pearson Correlation Coefficient R (p-value) 2004-07	WPBR Incidence: Pearson Correlation Coefficient R (p-value) 2016-17	Significant variables in mortality correlations	WPBR Mortality[b]: Pearson Correlation Coefficient R (p-value) 2016-17
Latitude (UTM)	0.241 (0.0361)	0.248 (0.0274)	**Longitude (UTM)**	0.228 (0.0425)
Slope * sin(aspect)	0.248 (0.0274)	0.252 (0.0249)	**Slope * sin(aspect)**	0.251 (0.0258)
Percent of ground cover that is vegetation	0.221 (0.0026)	0.145 (0.0301)	**Density of all species**	0.224 (0.0468)
Growing season precipitation	0.232 (0.0394)	0.219 (0.0522)	**Density of limber pine**	0.232 (0.0076)
Mean annual precipitation	0.269 (0.0165)	0.321 (0.0039)	**Basal area of live limber pine**	-0.200 (0.0761)
Diffuse short wave radiation	-0.324* (0.0035)	-0.263 (0.0198)	**Species composition that is "Other pines"**	0.316* (0.0046)
Derived short wave radiation	-0.341* (0.0021)	-0.345* (0.0019)	**Species composition that is "Spruce-Fir"**	0.236 (0.0354)
12 month moderate or greater drought frequency	-0.306* (0.0062)	-0.272 (0.0154)	**Mean annual temperature**	0.228 (0.0439)
Precipitation May	0.336* (0.0024)	0.317* (0.0009)	**Degree days <0°C**	-0.238 (0.0340)
Precipitation June	0.402* (0.0002)	0.388* (0.0004)	**Growing degree days**	0.242 (0.0319)
Precipitation July	0.247 (0.0282)	0.241 (0.0322)	**Average temperature in the warmest month (July)**	0.223 (0.0468)
Precipitation August	0.262 (0.0193)	0.263 (0.0191)	**Average temperature in the coldest month (Jan)**	0.247 (0.0279)
Precipitation September	0.296 (0.0079)	0.286 (0.0104)	**12 month moderate or greater drought frequency**	-0.336* (0.0025)
Relative Humidity June	0.270 (0.0159)	0.305 (0.0063)	**Ratio of growing season precipitation to annual precipitation**	0.268 (0.0169)
Relative humidity Sept	0.368* (0.0009)	0.341* (0.0021)	**Precipitation January**	-0.273 (0.0146)
Relative humidity Oct	0.295 (0.0082)	0.299 (0.0072)	**Precipitation July**	0.364* (0.0010)
			Precipitation November	-0.237 (0.0355)
			Precipitation December	-0.248 (0.0276)

[a] Only significant (p-value <0.05) correlations displayed
[b] Trees classified as "old dead" were not assessed in 2004-07 thus WPBR mortality values in 2004-07 are underestimated or zero
* asterisk indicates medium strength correlation (R > |0.3|)

Supplemental Table 14 – Regeneration (< 1.3 m tall) Species Composition of Sites

Study Area		Total # Stems All species		# Stems per Group – Live (Total) (Percent of # Stems - all species)[d]							
				Limber Pine		Other Pine[a]		Spruce-Fir[b]		Other spp.[c]	
		04-07	**16-17**	**04-07**	**16-17**	**04-07**	**16-17**	**04-07**	**16-17**	**04-07**	**16-17**
Overall		1025	1286	243 (23.7)	318 (24.7)	56 (5.5)	103 (8.0)	286 (27.9)	233 (18.1)	440 (42.9)	632 (49.1)
SOCO	Sangre de Cristo Mtns	**64**	**318**	**6 (9.4)**	**23 (7.2)**	**9 (14.1)**	**23 (7.2)**	**10 (15.6)**	**85 (26.7)**	39 (60.9)	187 (58.8)
COWY	Canyon Lakes	183	236	13 (7.1)	41 (17.4)	**16 (8.7)**	**29 (12.3)**	2 (1.1)	9 (3.8)	152 (83.1)	157 (66.5)
	Laramie Pk	129	178	61 (47.3)	77 (43.3)	6 (4.7)	3 (1.7)	20 (15.5)	42 (23.6)	42 (32.6)	56 (31.5)
	Pole Mtn	78	143	19 (24.4)	44 (30.8)	10 (12.8)	40 (28.0)	0 (0)	0 (0)	49 (62.8)	59 (41.3)
	Snowy Mtns	60	39	21 (35.0)	14 (35.9)	0 (0)	0 (0)	22 (36.7)	11 (28.2)	17 (28.3)	14 (35.9)
	Poudre South	28	23	8 (28.6)	4 (17.4)	6 (21.4)	3 (13.0)	7 (25.0)	3 (13.0)	7 (25.0)	13 (56.5)
NOWY	Shoshone	61	73	**40 (65.6)**	**59 (80.8)**	0 (0)	0 (0)	3 (4.9)	14 (19.2)	18 (29.5)	0 (0)
	Bighorn	85	83	9 (10.6)	6 (7.2)	9 (10.6)	5 (6.0)	37 (43.5)	30 (36.1)	30 (35.3)	42 (50.6)
MT		**331**	**193**	64 (19.3)	50 (25.9)	0 (0)	0 (0)	185 (55.9)	39 (20.2)	82 (24.8)	104 (53.9)
ND		**6**	**0**	2 (33.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (66.7)	0 (0)

[a] Other pine includes: *Pinus contorta* subsp. *latifolia*, *P. ponderosae, P. albicaulis, P. aristata*
[b] Spruce-Fir includes: *Pseudotsuga menziesii*, *Abies lasiocarpa*, *A. concolor, Picea engelmanni*
[c] Other spp. includes: *Juniperus scopulorum, Populus tremuloide*s
[d] Number of live stems per group divided by number of live stems for all species
Bolded values indicate significant change (p < 0.05) using McNemar's test from 2004-07 to 2016-17 within subregion

Supplemental Table 15 – Significant[a] Correlations in Limber Regeneration (< 1.3 m tall) to WPBR incidence/mortality

Variables in incidence correlations	WPBR Incidence Spearman's R (p-value) 2011-13	2016-17	Variables in mortality correlations	WPBR Mortality [b] Spearman's R (p-value) 2011-13	2016-17
Short wave radiation	**0.272 (0.015)**	-0.180 (0.112)	**Short wave radiation**	**0.260 (0.021)**	0.119 (0.295)
Water vapor pressure	**0.285 (0.011)**	0.204 (0.070)	**Water vapor pressure**	0.084 (0.458)	**0.367* (<0.001)**
Fertility index[b]	**-0.243 (0.030)**	-0.182 (0.011)	**Fertility index[b]**	-0.191 (0.091)	**-0.333* (0.002)**
Soil drainage index	-0.145 (0.201)	**-0.221 (0.049)**	**Soil component frequency**	0.080 (0.479)	**0.248 (0.027)**
Growing degree days	**0.289 (0.009)**	0.200 (0.076)	**Growing degree days**	0.181 (0.108)	**0.217 (0.048)**
Growing season precipitation	**0.270 (0.015)**	**0.266 (0.017)**	**Growing season precipitation**	0.184 (0.103)	**0.218 (0.047)**
Ratio of growing season degree days > 5°C to seasonal precipitation	-0.155 (0.178)	**-0.225 (0.046)**	**Ratio of growing season degree days > 5°C to seasonal precipitation**	-0.155 (0.170)	-0.118 (0.296)
Ratio of growing season precipitation to mean annual precipitation	**0.239 (0.033)**	**0.245 (0.029**	**Number of frost free days**	**0.218 (0.048)**	0.137 (0.225)
Precipitation July	**0.268 (0.016)**	**0.221 (0.047)**	**Precipitation July**	0.182 (0.106)	**0.242 (0.031)**
Precipitation August	**0.252 (0.025)**	**0.253 (0.024)**	**Precipitation August**	0.15 (0.201)	**0.277 (0.013)**
Precipitation December	**-0.236 (0.035)**	**-0.229 (0.041)**	**Precipitation December**	**-0.220 (0.049)**	-0.149 (0.187)
Relative humidity August	**0.271 (0.015)**	0.203 (0.072)	**Relative humidity August**	0.178 (0.116)	0.168 (0.138)
Relative humidity September	**0.328* (0.003)**	**0.314* (0.005)**	**Relative humidity September**	0.209 (0.063)	**0.311* (0.005)**
Average temperature in the coldest month (Jan)	**0.218 (0.048)**	0.186 (0.099)	**Density of limber pine [c] (stems ha^{-1})**	0.191 (0.091)	**0.242 (0.031)**
Average temperature Dec	**0.258 (0.021)**	**0.223 (0.047)**	**Total basal area of all tree species**	**0.224 (0.046)**	0.105 (0.356)
Minimum temperature in the coldest month (Jan)	**0.220 (0.049)**	0.185 (0.101)	**Species composition (%) that is "Other Species"**	-0.107 (0.344)	**-0.329* (0.003)**
Minimum temperature Dec	**0.256 (0.022)**	**0.216 (0.048)**			
Density of limber pine [c] (stems ha^{-1})	**0.256 (0.022)**	0.154 (0.174)			

[a] **Significant correlations (p-value <0.05) denoted in bold**
[b] Derived from SSURGO/STATSGO/NFS
[c] Both live and total (live + dead) limber pine density had significant correlation values
* asterisk indicates medium strength correlation (R > |0.3|)