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# Demographics and Growth History of Whitebark Pine on Undisturbed Sites Across the Northern US Rocky Mountains

Sarah Flanary

*University of Montana, Missoula*

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DEMOGRAPHICS AND GROWTH HISTORY OF WHITEBARK PINE  
ON UNDISTURBED SITES ACROSS THE NORTHERN US ROCKY  
MOUNTAINS

By

SARAH JEAN FLANARY

B.A. Communicative Sciences and Disorders, University of Montana, Missoula, MT, 2014

Thesis

presented in partial fulfillment of the requirements for the degree of

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Approved By:

Scott Whittenburg, Dean of the Graduate School

Dr. Edwin Burke

Department of Forest Management

Dr. David L.R. Affleck

Department of Forest Management

Dr. Ray Callaway

Division of Biological Sciences

## Demographics and growth history of whitebark pine on undisturbed sites across the northern US Rocky Mountains

Dr. Edwin Burke, Chair

Along with fluctuating precipitation and temperatures in the form of climate change, whitebark pine (*Pinus albicaulis*) has seen a territory wide increase in mortality leading to a decline in population. While the most direct influences on whitebark pine health and mortality are mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, fire exclusion policies, and the spread of white pine blister rust (*Cronartium ribicola*), climate change can impact the intervals and severity of such beetle, rust, and fire disturbances, and may affect the growth and health of whitebark pine directly. The objectives of this study were to identify whitebark pine stands within the northern US Rocky Mountains exhibiting low or no impacts of beetle attack and blister rust, to document the regeneration levels and structural components of these stands, and to examine the climatic controls on radial growth of the mature whitebark pine over the last 100 years. Across the high elevation forests of Montana, Idaho, and Wyoming, 92 minimally disturbed stands were identified. While free of blister rust and pine beetle damage, these stands still contained a high proportion of standing dead trees (24% of standing mature trees (>4.5" DBH) were dead on average). These stands also contained a high proportion of subalpine fir (on average, 14.4% of the mature tree density), but nonetheless exhibited high levels of whitebark pine regeneration (on average 1,195/acre below 4.5" DBH and 1,044/acre <4.5' in height). Tree ring growth analyses of the mature whitebark pine did not show any long-term trends, but inter-annual variations were positively correlated with growing season precipitation and negatively correlated with growing season temperatures. Tree ring indices also show that more recent radial growth rates are still within the range of variability for the 100 years sampled and do not appear to be decreasing with the increasing stress predicted by ongoing climate change. Over the same 100 years, yearly mean climate averages calculated using PRISM data attributed to the individual sites showed a range of 30.7° F for maximum temperatures, 40.2° F for minimum temperatures, and 97.03" for total precipitation.

## ACKNOWLEDGMENTS

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# 1 Introduction

Whitebark pine (*Pinus albicaulis* Engelmann) primarily occurs in subalpine environments in 7 US states and 2 Canadian provinces, encompassing about 18° of latitude and 21° longitude (Arno and Hoff 1990, Tomback and Achuff 2010). Within the Rocky Mountains, whitebark pine comprises 10-15% of the forested landscape and 25-50% of wilderness landscapes (Arno 1986, Keane 2000), and ranges in elevation from 1100 to 3660 meters (Arno and Hoff 1990).

Whitebark pine is currently undergoing a widespread decline throughout its territory as a result of interacting factors (Keane and Arno 1993, Kendall and Keane 2001, Goeking and Izlar 2018).

Severe mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, fire exclusion policies, and the spread of white pine blister rust (*Cronartium ribicola* Fischer) have greatly impacted whitebark populations across the Rocky Mountains (Keane and Arno 1993, Kendall and Keane 2001, Murray and Rasmussen 2003, Schwandt 2006, Tomback and Achuff 2010).

There is also growing concern over the role climate change will have in the longevity of the species, as many believe that whitebark pine will experience reduced growth and survival with the changing conditions and will be pushed to the tops of the mountains or further northward in latitude (Warwell, Rehfeldt et al. 2007, Schrag, Bunn et al. 2008). Attempts at assisted migration further northward have begun, as the rate of whitebark pine reproduction may be too slow to allow range expansion to keep pace with climate change (McLane and Aitken 2012). Species distribution models (SDMs) have predicted suitable territory for whitebark pine expansion in northern British Columbia; they have also shown that whitebark pine does not presently inhabit all currently predicted suitable habitat (Hamann and Wang 2006, McLane and Aitken 2012).

This may be due to lack of seed caching area for the mutualist disperser, Clark's nutcracker (*Nucifraga columbiana* Wilson), low snowpack, and early snowmelt (McLane and Aitken 2012).

Paleoecological records show that whitebark pine has maintained and even spread in warmer and drier climates in the past (Tausch, Wigand et al. 1993, Whitlock and Bartlein 1993, Iglesias, Krause et al. 2015). Arno (1990) demonstrated that in the Bitterroot Mountains of Montana, whitebark pine extended another 500 feet below the species' current elevational range when there have been frequent historic disturbances, such as fire or insect kill, that eliminated less tolerant conifer species (Arno and Hoff 1990, Arno 1990, Keane and Arno 1993). Whitebark pine is tolerant of a variety of growing conditions, although it is primarily climax only at the higher elevations where there is little competition and successional relationships with other species. Changing fire regimes have had the greatest effect on habitat suitability, and many higher elevation whitebark pine stands have been supplanted with late seral subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) (Tomback, Arno et al. 2001). Whitebark pines' low to moderate fire severity tolerance (Ryan and Reinhardt 1988) and specialized seed dispersal technique involving its mutualistic relationship with the Clark's nutcracker allow for the pine species to thrive in areas with mixed severity fire regimes, which have decreased since the implementation of fire suppression (Tomback, Arno et al. 2001, Wood 2015).

The elimination or reduction of this species on the landscape will have broad reaching consequences for ecosystem services and biodiversity (Tomback, Arno et al. 2001, Tomback and Achuff 2010). Whitebark pine cone seeds are higher in fat and protein content than other conifer seeds and are an important food source for the Clark's nutcracker, the grizzly bear (*Ursus arctos*), and other small mammals. Whitebark pine also provides significant habitat for many animal species. As whitebark pine are able to grow under harsher conditions, they are often the first to inhabit an area as a pioneer species, and provide shade and other services to less hardy vegetation and conifer species, acting as nurse trees and resulting in "island" growth formations



(Callaway 1998). Whitebark pines also reduce soil erosion and regulate snow melt rates through root structure and shade effects (Tomback, Arno et al. 2001).

Despite the consequences from the potential loss of this species from the landscape and its recent inclusion as a candidate species under the Endangered Species Act (USFWS 2011), there have been few studies of the effect of climate change on whitebark pine growth and ecology. Speculation has anticipated that whitebark pine could foreseeably be “pushed” off the tops of mountains as climate related habitat expansion ascends upwards in elevation, while statistical modeling has predicted everything from dramatic decreases to sustained populations as a result of factors such as high genetic diversity, increasing fire on the landscape, blister rust resistance, and other key adaptive traits (Keane 2001, Loehman, Clark et al. 2011). High genetic diversity, as is typical of long-lived trees such as whitebark pine, is predicted to make species more resilient to drought, while increasing fire on the landscape would increase potential cache sites for the nutcracker as well as destroy less fire-tolerant competitor species (Mitton 1995, Hamrick 2004, McDowell, Pockman et al. 2008, Keane, Holsinger et al. 2017). Case and Lawler (2016) looked at 11 different conifer species’ vulnerabilities to climate change and listed whitebark pine as highly sensitive to climate change based on its relationship with interacting non-climatic stressors (habitat loss or degradation, dispersal limitations, invasive species etc.), and indicated it should be considered vulnerable. Population dispersion and sustainability are dependent on a wide variety of variables; thus it is hard to predict the species’ future with a high degree of certainty. There are currently no ecophysiological models that accurately predict whitebark pine mortality and spread, and consequently the current study relies on direct empirical observation of tree and plot dynamics as well as current generation climate data products.

With mixed concerns over the projected success of whitebark pine under a changing climate, stand composition and regeneration is of interest. Whitebark pine has historically inhabited harsh environments near the upper tree line. These areas carried the heavier snowpack with a later melt date, giving any established seedlings a shorter growing season. Climate change is lengthening the growing season, and this combined with fire suppression policies implemented by the U.S. Forest Service in the early 1900's has increased the success rate of competitor conifer species seedlings, which frequently have faster growing rates than whitebark pine (Arno 1989, Alexander, Shearer et al. 1990, Easterling 2002, Linderholm 2006, Karl, Melillo et al. 2009, Levine, Krivak-Tetley et al. 2016). Goeking and Izlar (2018), using national forest inventory data, identified that as of 2016, 51% of all standing whitebark pine within the United States were dead (292 million live and 308 million dead). Other work identified that whitebark pine habitats had upwards to 74% mortality in the Northern Divide Ecosystem within the Rocky Mountains, and concerns have been raised about the presence of enough healthy, cone bearing adults to maintain the viability of the species (Fiedler and McKinney 2014, Leirfallom, Keane et al. 2015, Miles 2016, Goeking and Izlar 2018). Also, climatic conditions that encourage mature tree stem development are different than those that may encourage seedling growth, and seedlings, with their more sensitive response to daily conditions, may not survive at historic rates under novel climates (Day, Greenwood et al. 2002, Körner 2012, Dolanc, Westfall et al. 2013, Millar, Westfall et al. 2015).

As most of the models predicting future whitebark pine range are calling for a continuing steep decline in population, it is critical to understand and document current patterns of mortality and regeneration in stands undisturbed by beetles, rust, or fire. Moreover, at such undisturbed sites it is important to understand the relationship between historical climate and the vigor of mature trees.

As such, the objectives of this study were to identify undisturbed whitebark pine sites across the US Rocky Mountains, quantify current mortality and regeneration levels, and use dendrochronological methods to identify relationships between mature tree growth and climate over the period for which temperature and precipitation can be estimated.

## **2 Study Area and Methods**

### **2.1 Study Area and Data Collection**

For this project, the study area encompassed a series of mountain ranges across Montana, Idaho, and Wyoming in which whitebark pine is found (Figure 1). Local knowledge through communications with Forest Service district personnel as well as GIS methodology were used to identify sites within this area that had not been subject to multiple wildfires or high mortality from insects or disease. Sites also needed to be within 2 miles of a road to facilitate access, to exhibit no signs of heavy agricultural or human use (such as intense cattle grazing or soil compaction from human recreation), and to show no sign of harvesting for timber or firewood.

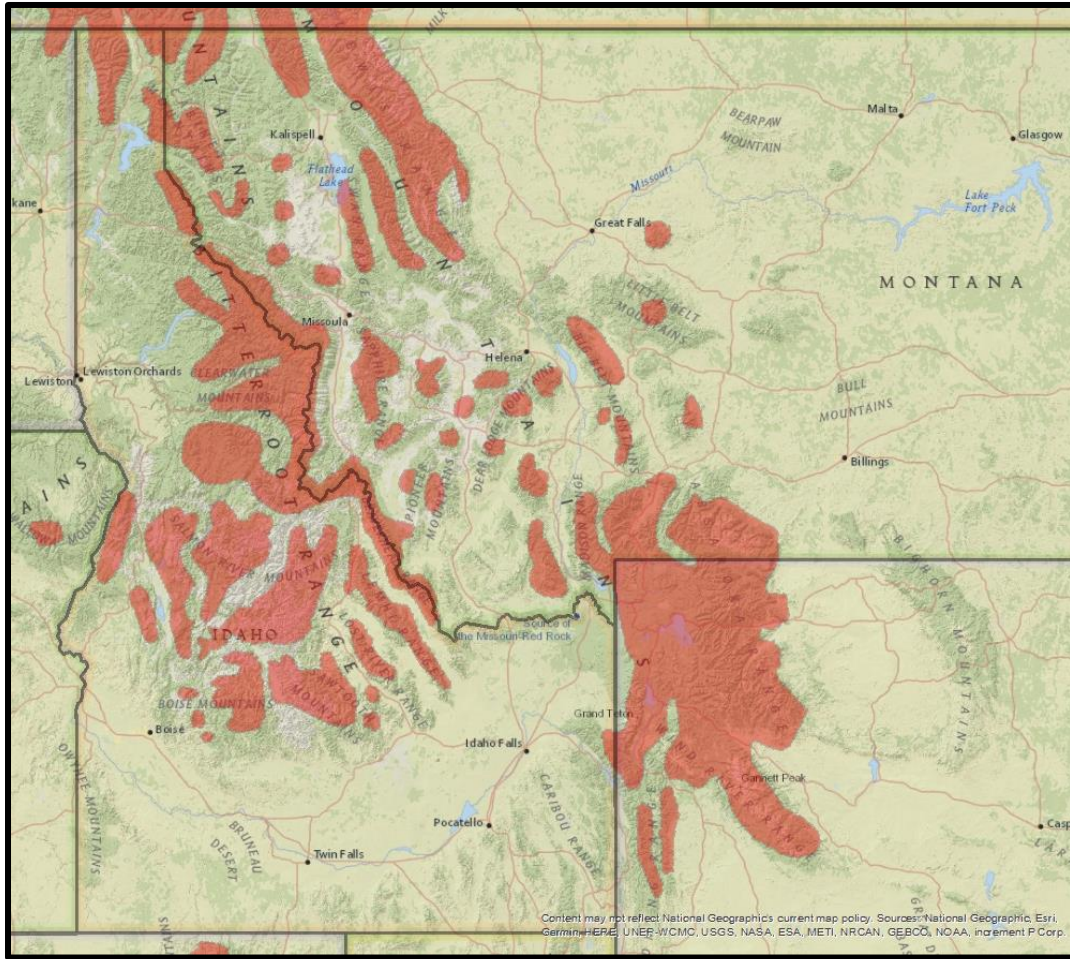


Figure 1: Range of whitebark pine (*Pinus albicaulis*) in the northern US Rocky Mountains.

At the selected minimally disturbed sites, a nested plot design was used to collect vegetation data. The circular plots each had a radius of 37.2 feet, comprising 1/10<sup>th</sup> acre of land. The center was temporarily marked with a chaining pin and cloth tapes were spread out in cardinal directions for sampling distances. Plot information was recorded using the FIREMON methods (Lutes, Keane et al. 2006). GPS coordinates were taken, and aspect, slope, and elevation noted. Mature trees, sampled on the full 1/10<sup>th</sup> acre plot, were considered such if they were larger than 4.5 inches in diameter at breast height (DBH, taken at 4.5 feet distance from ground on uphill side of tree). For mature trees, DBH, species, height, health, percent live crown, and live crown

distance from ground were recorded. For dead trees, the above details were recorded as well as decay class and visual assessments of mortality agent. Decay classes ranged from a 1 to 5, with 1 being recently dead and possessing needles, fine twigs, and bark, and 5 having no branches or bark, and frequently missing the top of the snag. Saplings, considered to be anything taller than 4.5 feet but less than 4.5 in DBH, were measured as well on the 1/10<sup>th</sup> acre plot, with species, height class, and distance from ground to live crown being recorded. Seedling plots of 1/300<sup>th</sup> acre in size and comprised of trees shorter than 4.5 feet were also installed. Vegetation and ground cover data were recorded within the plot using FIREMON (Lutes, Keane et al. 2006) and Photoload methods (Keane and Dickinson 2007). Descriptive statistics of mortality rates and regeneration levels were calculated from the plot data. Patterns in mortality and regeneration levels were examined on a stand and regional level and in relation to site characteristics.

## **2.2. Climate Data Products**

Data products from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group were obtained for monthly maximum and minimum temperatures, and monthly precipitation, from 1915 to 2015, using R-Studio and ARCGIS (Daly 2004, ArcGIS 2012, Team 2015). As historical PRISM data products had to be used, the spatial resolution of the climate variables was limited (4 km x 4 km grid database) (Daly 2004). Palmer Modified Drought Index (PDMI) data products were also downloaded for the individual sites (Cook, Seager et al. 2010).

## **2.3. Core Sampling and Data Extraction**

From the mature trees measured on each site, core samples were taken 1 foot from the ground from 2-3 of the mature whitebark pine, as well as from one other mature tree if a

different species was available. Cored trees were selected based on health, presence of cones as an indicator of maturity, and accessibility to stem for coring. Sapling and seedlings were also cored if available on the plot.

The cores that were taken were brought back to the lab and stored in a warm, dry place until they could be processed. Cores were mounted and sanded down to 9 micron or until rings were clearly visible. Using a high-resolution scanner, the individual cores were scanned in at 3600 dots per inch (DPI) and an image saved for each. Using the images, ring widths were then measured to the pith or last ring available using the program CooRecorder (Larsson 2014). Some cores were unable to be used due to factors such as breakage or rot.

Cores measured within the program CooRecorder were grouped by site for cross dating within the program CDendro (Larsson 2014). Cross dating is generally done using a master chronology for comparison, but there are very few relevant published chronologies within the areas sampled. The ring width data were normalized within CDendro for crossdating purposes, and the raw data then read into R-studio using the package “dplr” (Bunn 2008, Team 2015). Raw ring widths were then detrended using a modified negative exponential approach, which attempts to remove any biological growth difference attributable to tree age or size, and then the detrended ring widths were saved as individual ring width index ( $RWI_{tree}$ ) files. The chronologies for each site were then built using the detrended  $RWI_{tree}$  files with Tukey’s robust mean, and a site-level ring width index ( $RWI_{site}$ ) chronology saved for each (Tukey 1977). The indices for the sites are created by dividing the observed value by the predicted ring width value, resulting in homogenous variance around a mean of 1.  $RWI_{site}$  chronologies with interseries correlation values  $\geq 0.30$  were combined into an overall mean RWI chronology,  $RWI_{region}$ .

Following the ring width work, a growth-climate variable analysis was performed using the function “dcc” from the R package “treeclim” on the individual  $RWI_{site}$  chronologies to examine the relationship between the climate product variables and growth on the sites (Zang and Biondi 2015). This carried out a stationary bootstrapped correlation analysis and calculated Pearson’s correlation coefficient values for each site and the site specific climate variables, which were monthly precipitation, maximum temperature, and minimum temperature from prior year June to current year September (Pearson 1895, Politis and Romano 1994).

# 3 Results

## 3.1 Distribution of study sites

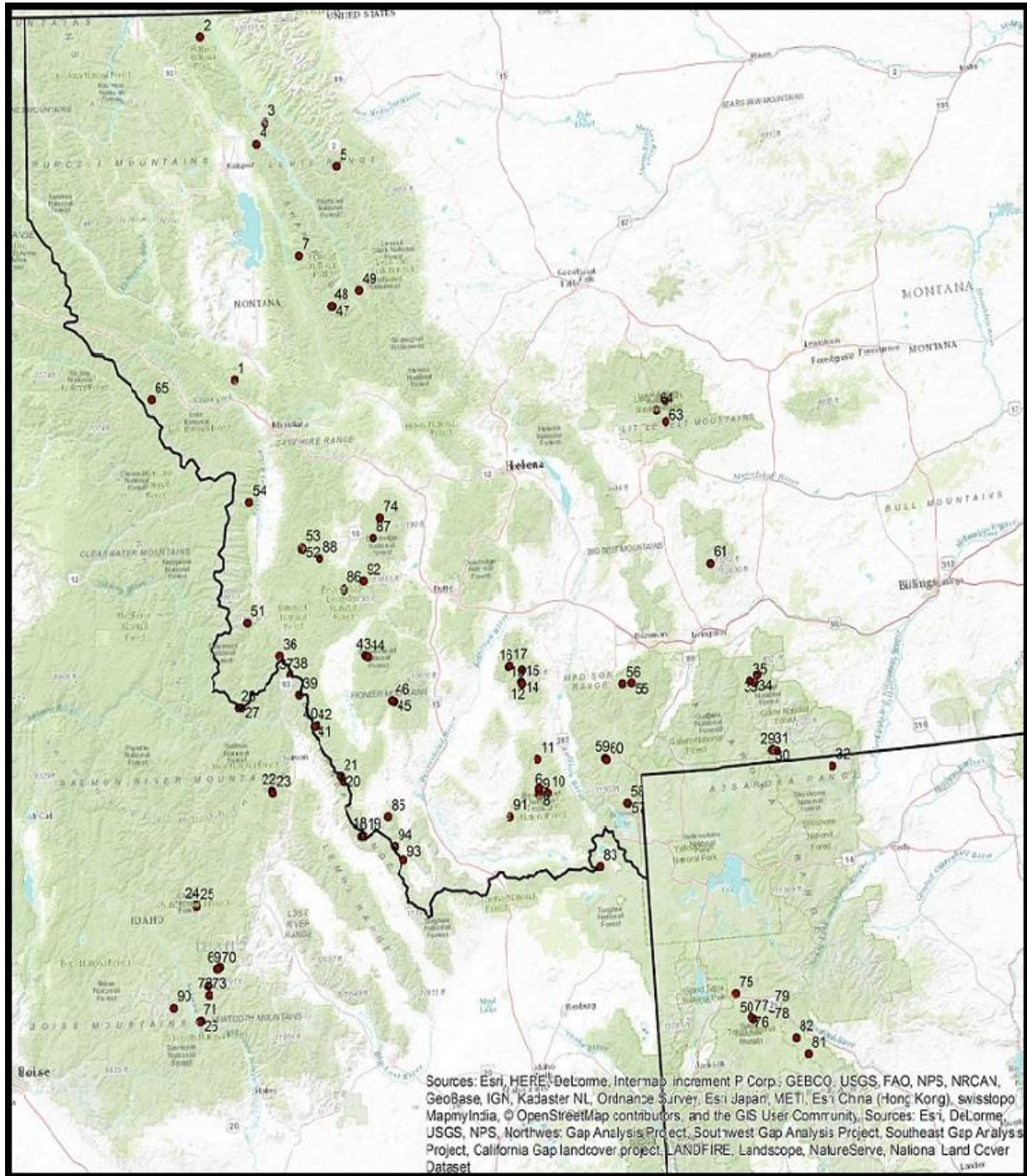


Figure 2: Map of numbered sites and their locations used for study.



Ninety-two minimally disturbed whitebark pine sites were located throughout the northern Rocky Mountains (Figure 2). Sites were distributed across varying aspects and slopes, but the majority of sites were between 8,001 and 9,500 feet in elevation (65 of the 92 sites). Mature tree basal area (BA) when all species were combined encompassed a range of 25 to 400 ft<sup>2</sup>/acre. Of the sites sampled, 36 were a subalpine fir habitat type (Pfister 1977), although in only 21 sites were whitebark pine not the dominant species in the canopy. Located sites had not experienced fire in at least 40 years and had no current white pine blister rust indicators or sign of mountain pine beetle attacks. They also had no recent disturbance from humans, although several sites had scattered stumps from trees that had been harvested decades ago (identified as such by decomposition assessments) or signs of cattle grazing in the undergrowth. Sites ranged from open growth grassy stands that had only 20 mature (> 4.5 inches at DBH) trees per acre with no sampled regeneration, to sites that were heavily mixed conifer types of predominantly subalpine fir and lodgepole pine, to higher elevation whitebark pine climax stands, with undergrowth of *Carex geyeri* and/or *Vaccinium scoparium* and other commonly associated species (Figure 3, Table 1, Table A1). Spatially, the sites were located from just outside the north-west corner of Glacier National Park, only a few miles from Canada, to the southern end of the Wind River Range in Wyoming. While the sites themselves had minimal disturbance, they were frequently located very near, or within, larger stands that had experienced disturbance, mostly commonly white pine blister rust.





Figure 3: Photo series from sampled sites showing the variety among stand types. A) Site 81- Open growth, low basal area stand with grass dominant undergrowth. B) Site 48- Mixed conifer stand with moderate shrub undergrowth. C) Site 32- Pure whitebark pine stand with *Vaccinium scoparium* undergrowth

	Mean	Minimum	Maximum	Standard deviation
<b>Elevation (ft)</b>	8402	6342	10090	812
<b>Mature tree total BA (ft<sup>2</sup>/acre)</b>	144	25	400	71
<b>Mature whitebark BA (ft<sup>2</sup>/acre)</b>	100	8	309	66
<b>Mature tree density (# per acre)</b>	287	40	790	132
<b>Mature whitebark pine density (# per acre)</b>	187	20	770	133
<b>All seedling density (# per acre)</b>	4754	0	29268	7311
<b>Whitebark pine seedling density (# per acre)</b>	1054	0	9756	1699
<b>Mature whitebark pine height (ft)</b>	36	19	62	10

Table 1: Descriptive range of site characteristics. Basal area (BA) and density counts include both live and dead combined.

### **3.2. Mortality on Sites Sampled**

There were no spatial patterns in the snag density. When snag data was split into visually estimated decay classes (1 being recently dead, 5 having no bark and no limbs or limb stubs), whitebark pine snags were further decayed than other conifer species present, suggesting they had been dead longer (Table 2). When the density data for whitebark pine snags was plotted against live basal area of the sites there was not an increased number of dead with increasing basal area (Figure 4). When the density of standing dead whitebark pine for each site were plotted against non-whitebark pine live basal area of the sites, there was no positive correlation in the number of whitebark pine snags, suggesting that regardless of the basal area of faster growing conifer species, mature whitebark pine on these minimally disturbed sites sampled are not experiencing an increase in mortality numbers due to competition.

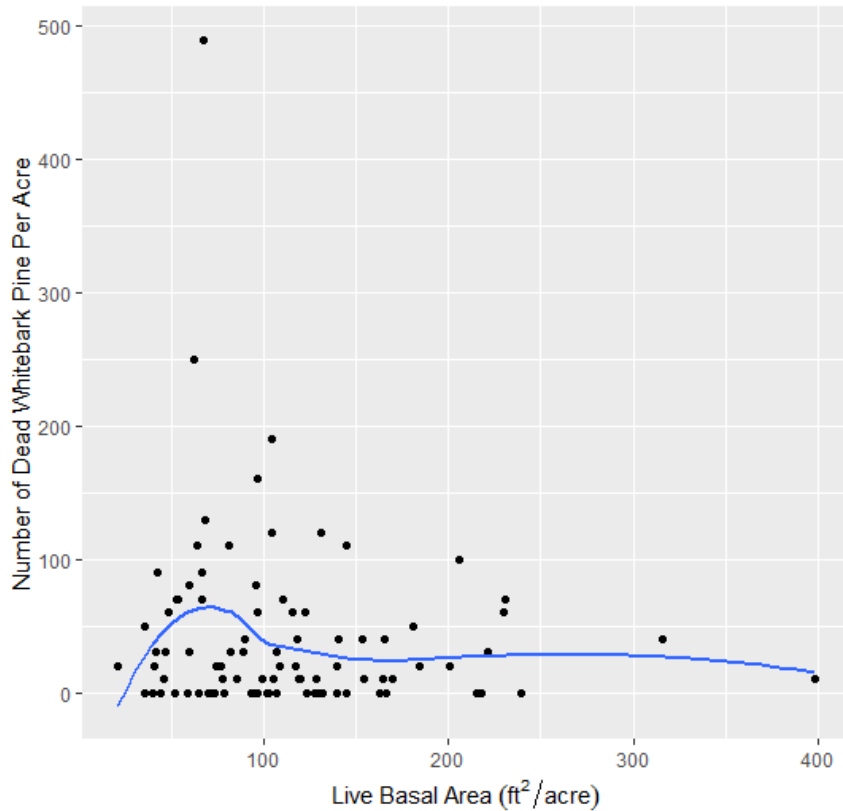


Figure 4: Density of whitebark pine snags against live mature basal area (all conifer species combined).

Sites chosen for the study had minimal disturbance from blister rust or beetle epidemics. A Welch’s t-test found there to be a difference in the average snag counts (p-value=0.002, t=3.176) when separated into whitebark and “other conifers” categories. Of the 92 sites, 20 had no snags at all, and decay class data was only available for the snags on 40 of the residual 72 plots due to a change in sampling technique. Number of total snags on each site, when all conifer species were combined, ranged from 0 up to 49 snags.

Species	Total # sampled snags	Ave. # dead per site	Ave. BA/acre dead (ft <sup>2</sup> )	% in decay classes 1-2	Ave. # live trees per site	Ave. % dead within site	SE for % dead each site	SE for # dead per site	SE for # live per site
<b>Whitebark</b>	357	3.88	32	51%	16	24%	1.6	0.7	1.11
<b>Other conifers</b>	137	1.16	23	88%	9	16%	0.68	0.24	0.91

Table 2: Sites sampled were 1/10<sup>th</sup> acre in size. Species refers to whitebark pine or a grouping of other conifers sampled within the 92 plots (subalpine fir, lodgepole pine, Engelmann spruce, Douglas fir). Counts and percentages are from all 92 plots combined. Decay class is from 1-5, with 1 being the most recently dead and 5 has been dead the longest. % decay class on snags is from 40 out of the 72 sites with snags.

### 3.3. Stand Composition and Regeneration

While mature whitebark pine are still the most prevalent species on the sites, their relative representation within the sites decreased through the structural stages of saplings and seedlings. At the same time, there is a relative increase in the abundance of subalpine fir in the structural stages of sapling and seedlings. When the data were examined among all structural stages (Figure 5), whitebark pine was the most abundant species in the mature stage, however, there were fewer seedlings of whitebark pine than of subalpine fir. Over the 92 sites, whitebark pine seedlings were found on 47 and subalpine fir seedlings on 46. On sites that had subalpine fir seedlings, increasing mature whitebark pine basal area was negatively related to subalpine fir seedling counts.

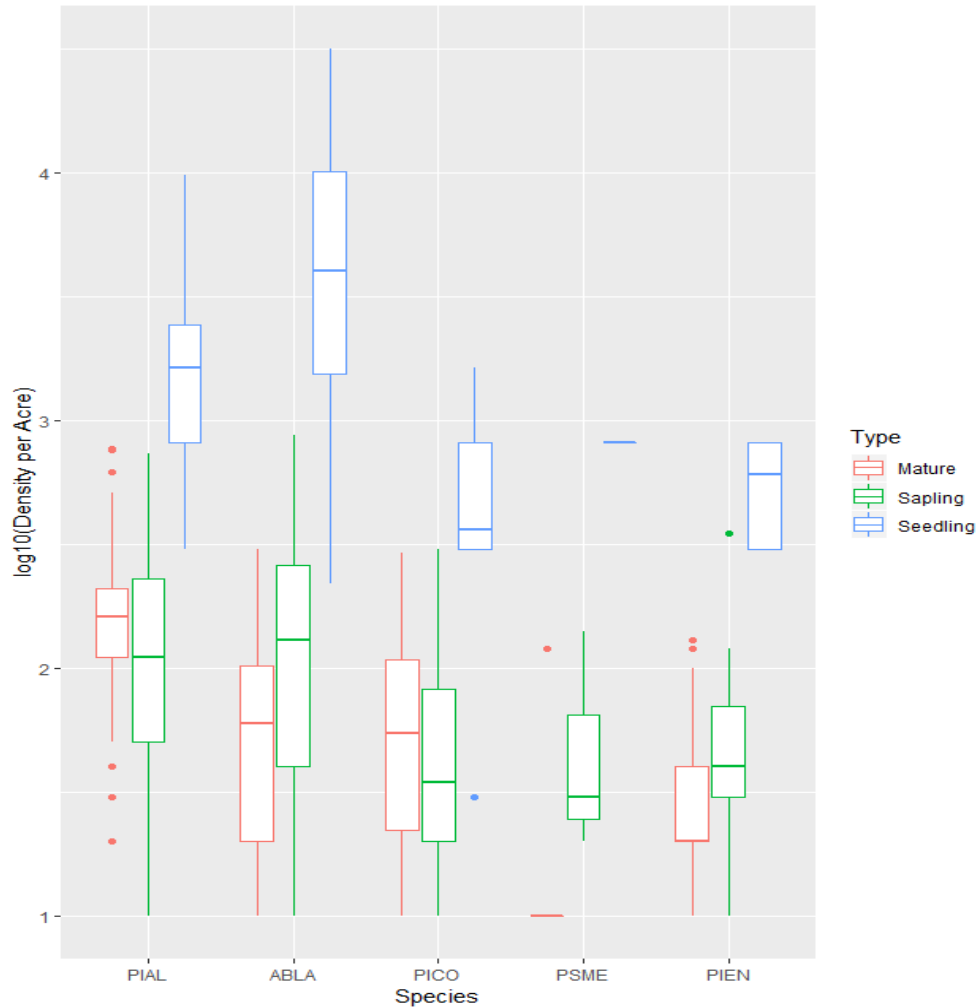


Figure 5: Boxplot showing the log10 density per acre (live only) of the 5 most prevalent species found within the sites sampled. Numbers were calculated for every site individually, within the type of species and structural stage (mature, sapling, seedling).

Correlation matrices using seedling and sapling totals for each site and the biophysical site characteristics revealed no relationships when all species were combined. Total mature tree density, all species included, was significantly correlated at an  $\alpha < 0.05$  level with increasing elevation and latitude. When the data were separated by species and structural stage and mapped to examine any potential spatial trends, whitebark pine showed more of a proportional presence among all structural stages the further south the plots were within the sampled region, and when

structural stages were combined was significantly correlated with latitude, longitude, and elevation at  $\alpha \leq 0.05$ . Sites further north tended to have more subalpine fir, though the relationship was not significant at an  $\alpha \leq 0.05$  level. When whitebark pine regeneration density (seedlings and saplings combined) was plotted against mature live basal area from all species combined (as well as against only non-whitebark pine species), whitebark pine regeneration density showed a tendency to increase with mature live basal area (Figure 6). However, there was substantial variability in whitebark pine regeneration levels and this relationship to live basal area density was not significant.

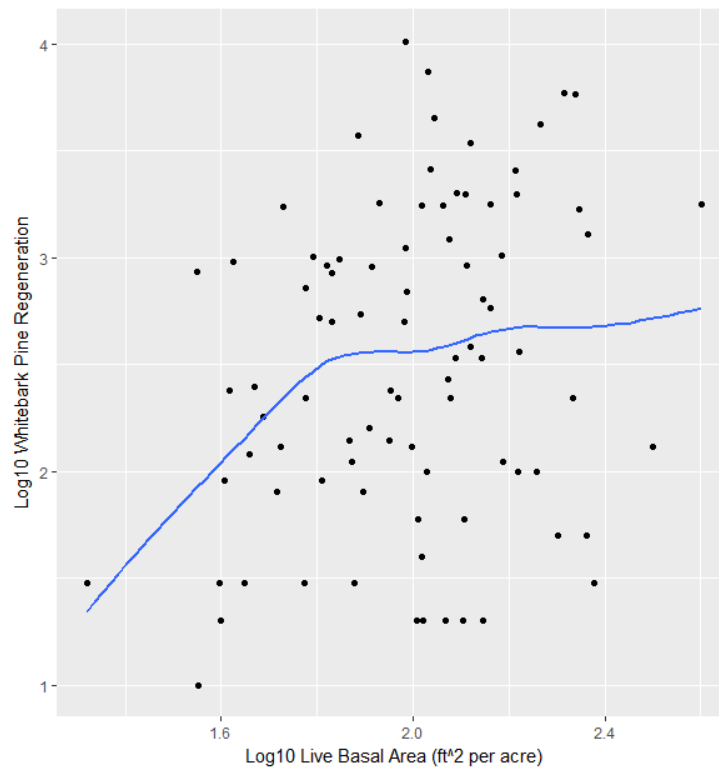


Figure 6: Log10 whitebark pine regeneration (seedlings and saplings combined) plotted against log10 live basal area (ft<sup>2</sup>/ac) when all mature conifers were combined.



For this study, structural stages were defined by their height and DBH. Using data from all sites combined, mean number per acre of whitebark pine by height class were calculated and plotted (Figure 7). The figure reveals the overall high density of whitebark pine seedlings, particularly those under 4 feet in height. Saplings and mature trees, distinguished by DBH, share height class categories from 6 to 28 feet in height, and there is a decline in abundance as the height classes increase.

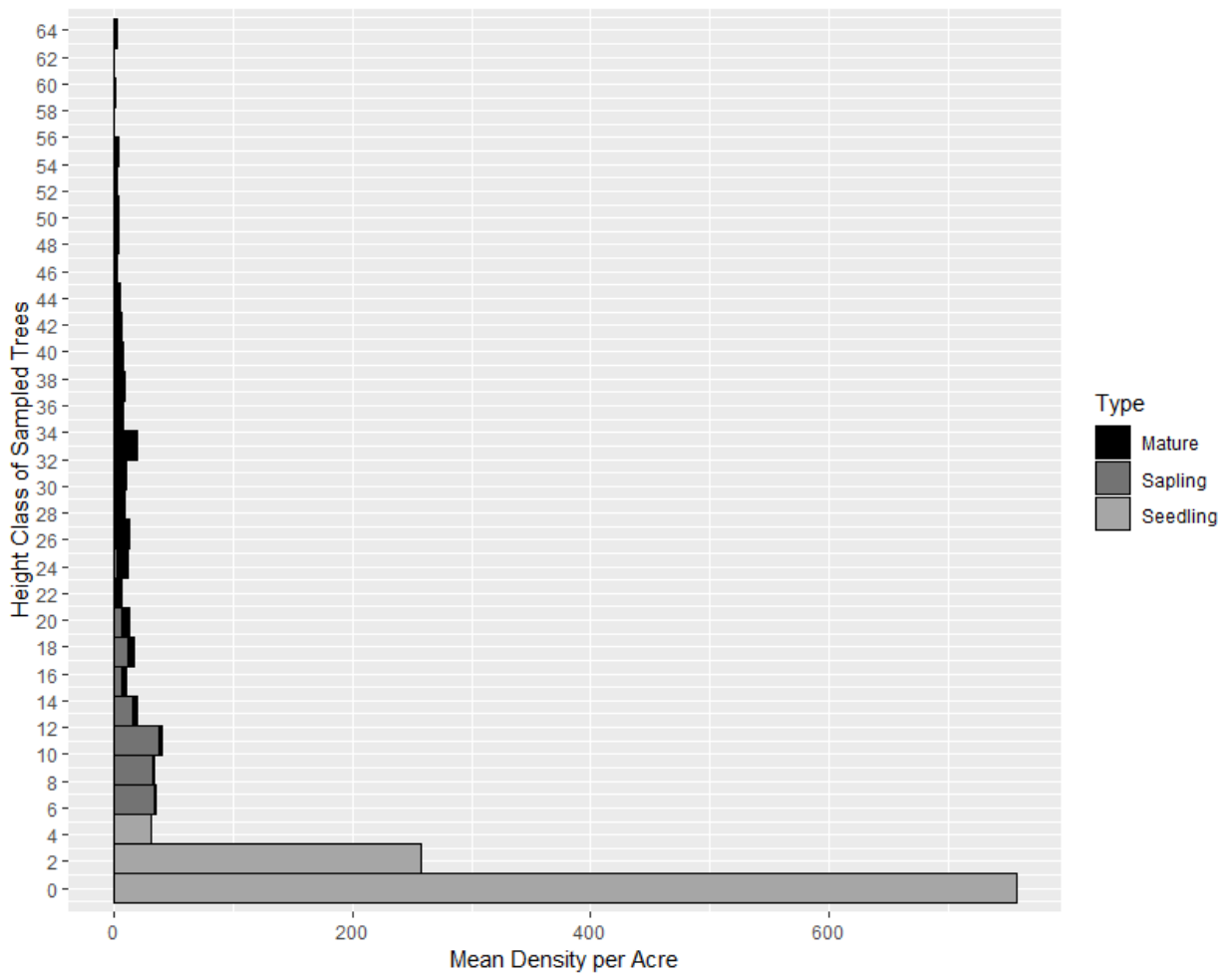


Figure 7: Height (ft) distribution of whitebark pine across all sites by structural class.

Across all sites, 98 whitebark pine seedlings and saplings above 6 inches in height were cored to examine the relationship between height and establishment date. This was done to

examine whether the seedlings and saplings were actually young trees or whether they had persisted in these structural stages over longer periods, as whitebark pine can have extremely slow growth (Figure 8) (Tomback, Sund et al. 1993, Campbell and Antos 2003, Leirfallom, Keane et al. 2015). Figure 8 shows the distribution of seedling and sapling establishment dates and highlights that 58% of these trees below 4.5 inches in DBH are more than 50 years old. The apparent decrease in numbers established over the most recent two decades is likely a result of the fact that only seedlings and saplings greater than 6 inches in height were cored for age.

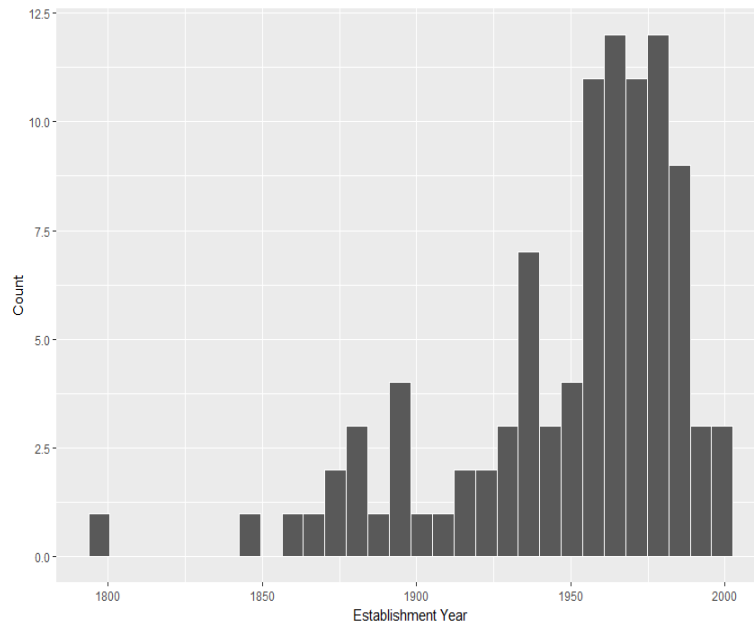


Figure 8: Histogram plot of establishment dates for subsampled whitebark regeneration (seedlings and saplings above 6 inches in height)

### 3.4. Climate and Ring Width Growth

Examining the climate data products used for the sites sampled, minimum temperatures fluctuated considerably from 1915-1990, but show both an increase in level and a decrease in

inter-annual variability after 1990 (Figure 9). No such pattern is evident in maximum temperature, precipitation, or Palmer Modified Drought Index (PDMI). Precipitation appears to have been declining for the prior 30 years from sampling date but is still within levels similar to the period from 1920-1950. There was a larger decline in  $RWI_{\text{region}}$  (the mean of all site chronologies) growth starting in 1998 and running through 2004 than any period prior, but in 2004 growth began to increase again. When visually comparing  $RWI_{\text{region}}$  against the climate variables,  $RWI_{\text{region}}$  does appear to respond to the recently warming minimum temperatures and dropping precipitation. The cores sampled for this study also had mostly high first-order autocorrelation scores in their raw ring widths, ranging from 0.17 to 0.94 with a mean of 0.7 (Fritts 1976).

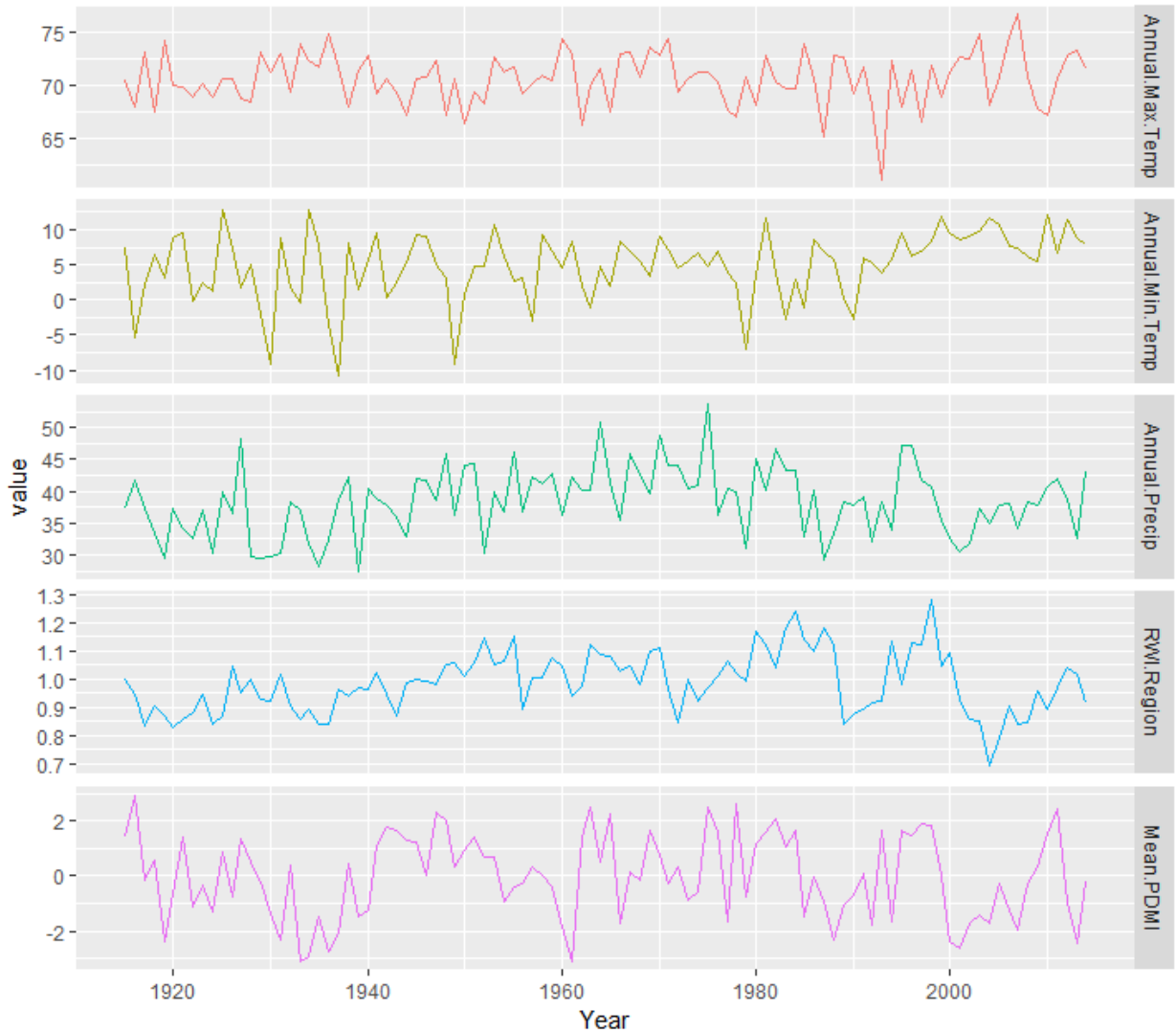


Figure 9: Mean values for annual maximum temperature ( $^{\circ}\text{F}$ ), annual minimum temperature ( $^{\circ}\text{F}$ ), total annual precipitation (inches), annual ring-width index ( $\text{RWI}_{\text{region}}$ ) and annual Palmer Modified Drought Index (PDMI). All variables have been averaged across all 92 sites.

When the ring-width index data ( $\text{RWI}_{\text{site}}$ ) for sites with interseries correlation values of  $>0.3$  were plotted, there was no apparent trend over the 100 years of growth data available (Figure 9). As noted above, beginning in 1998 there is a sustained decrease in ring-width index values, but  $\text{RWI}_{\text{site}}$  value and the overall  $\text{RWI}_{\text{region}}$  value begin to increase again around 2004, with one plot showing greatly increased growth, for which a cause has yet to be determined.

RWI Chronology Across Sites Sampled (1915 - 2014)

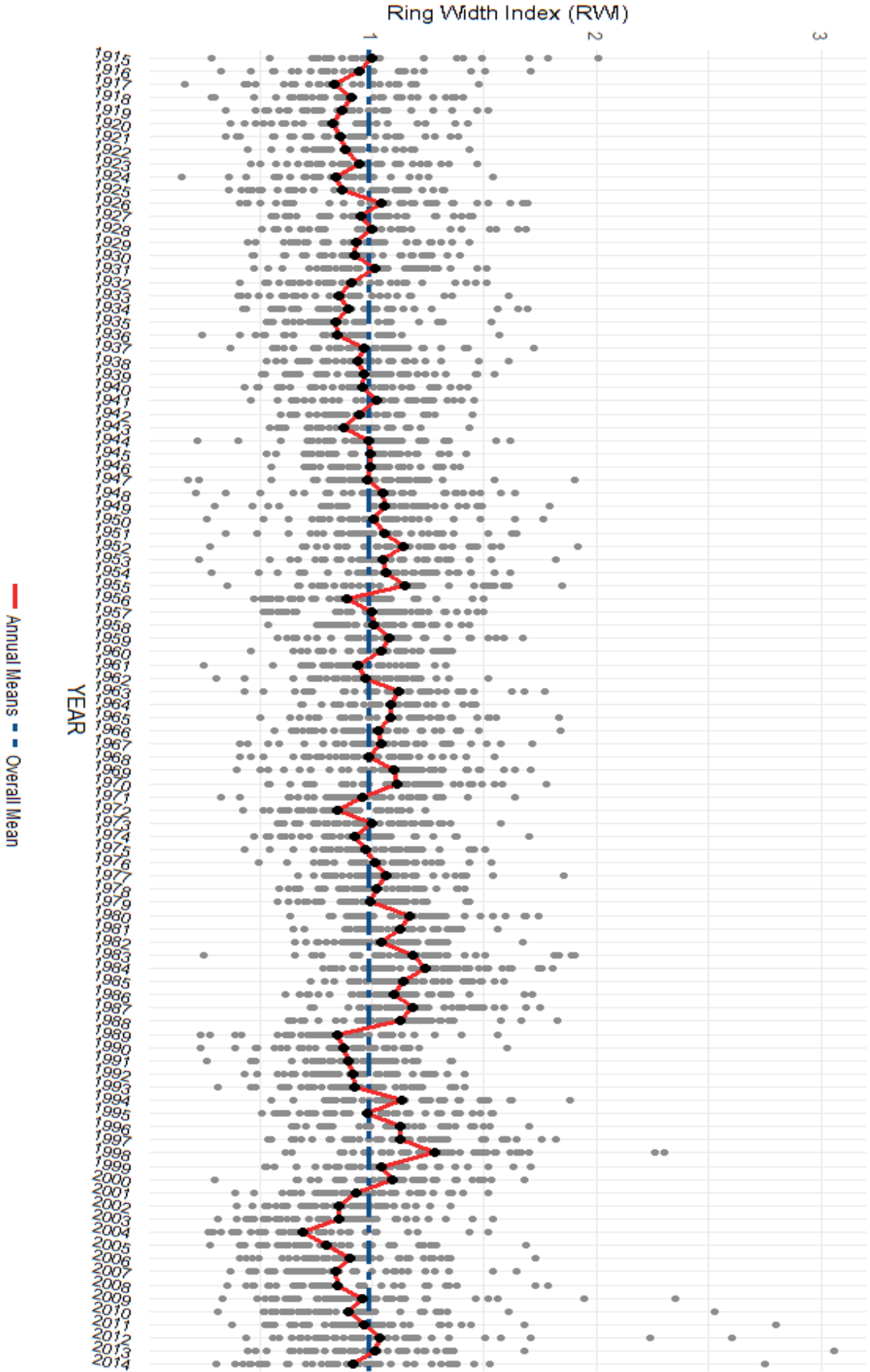


Figure 10: Distribution of ring width indices 1915-2014 by site (points); red line traces the regional average ( $RWI_{region}$ ). Only data from sites with interseries correlations  $>0.3$  were used.

Dendroclimatic calibration between monthly climate variables and  $RWI_{site}$  demonstrated that precipitation was positively correlated with  $RWI_{site}$  on average 67% of the 16 months used in the analysis, in particular during the prior and current year growing season months. Temperature data was mostly negatively correlated with  $RWI_{site}$  (on average, 78% of the time), with stronger correlations during the growing season (Figure 10). Overall, previous and current year July climate data products had the strongest correlations with radial growth (both  $RWI_{site}$  and  $RWI_{region}$ ), with current year March showing stronger correlation values with radial growth as well.

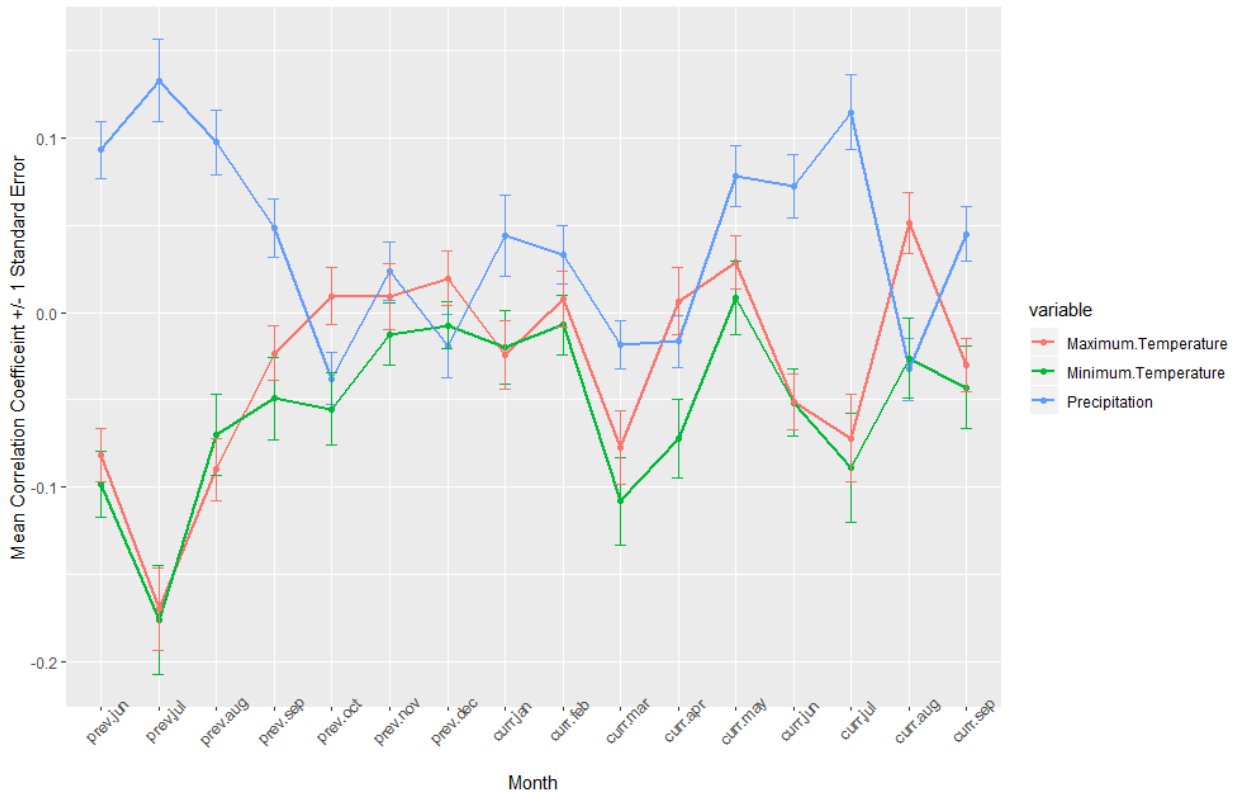


Figure 11: Correlations between  $RWI_{site}$  and monthly climate variables averaged over all sites and years (1916-2014). Shown are correlations for monthly climate variables running from the previous year's June through the current year's September.

Monthly climate data products were also plotted individually in an effort to determine how they may have changed over time. Generally, they showed temporal trends similar to the annual climate variables (Figure 9), with increasing minimum temperatures of 4-7 °F and an overall decrease in precipitation since the 1980s. Monthly maximum temperatures increased only a few degrees in all months except for in March, in which maximum temperatures among the sites sampled increased almost 5°F over the 100 years examined. Averaged monthly precipitation totals for the sites decreased in the last several decades through the months of February and March, as well as mid-summer, while increasing in the late fall and early winter months.

## 4 Discussion

Whitebark pine is continuing to see drastic population declines over much of its habitat, but there are sites and stands that have remained relatively undisturbed through recent mountain pine beetle epidemics and persistent blister-rust spread. Over a range of habitat types, climate, and biophysical site characteristics within the northern Rocky Mountains, whitebark pine populations with lower stand mortality exist on these minimally disturbed sites. Whether they have maintained their status due to location, luck, or some unmeasured phenological attribute could not be determined in this study, but they do provide a potential seed source for surrounding areas experiencing higher mortality. However, Table 2 represents the fact that even on these sites with lesser mortality, that the average percent dead is still roughly 25%. While there is no

existing snag dynamic information available for whitebark pine, the visual decay estimations performed for this study quantified 49% of the snags subsampled for extra data as being a decay class 3 or higher, which is attributed in general to snags not recently dead. This data presents the possibility that many of the snags present on the sites may be remnants of mortality decades past.

Climate conditions that promote the growth of mature trees may be different than those that promote seedling growth, thus seedlings may not survive microsite environmental conditions that have no effect on the ring production of mature trees. If the soil temperatures are too high, mortality rates increase, as the roots are sensitive, especially immediately post-germination (Rocheport, Little et al. 1994). Warming temperatures may not ensure sufficiently long cold stratification periods for germination, and may result in lower survival rates for those that do germinate (Arno and Hoff 1990). Prior studies have found that whitebark pine seedlings show improved growth and survival with higher precipitation amounts through March and April, and in fire disturbed areas (Tomback, Sund et al. 1993, Day, Greenwood et al. 2002, Körner 2012, Dolanc, Westfall et al. 2013, Millar, Westfall et al. 2015, Perkins 2015). Knowing these specifications, within the sites sampled, climate data products and projections indicate that minimum temperatures are increasing and the favorable spring precipitation decreasing (Leung, Qian et al. 2004, Iglesias, Krause et al. 2015).

The proportion and number of subalpine fir seedlings and saplings measured on the sites are higher than whitebark pine (Figure 5). Others research has found a similar relationship when both species were present, with whitebark pine seedling numbers decreasing with increased subalpine fir presence (Larson and Kipfmüller 2010). Changing climate and fire disturbance regimes to eliminate the quickly growing, more shade tolerant competition conifer species may be assisting in declining whitebark pine presence. As well, fire severity and scope may be



resulting in fewer of the Clark's nutcracker preferred seed caching sites, and high mortality related to white pine blister rust and mountain pine beetle may provide for poorer seed sources. These combined factors lend to future predictions of decreasing regeneration of whitebark pine. However, the broad distribution of whitebark pine among varying habitat types and biophysical site characteristics (Figure 1, Table A1), as well as the species' long lifespan, may allow it to continue as part of mixed-conifer stands. A recent study examining occurrence of whitebark pine seedlings found that within the US Rocky Mountains, whitebark pine seedlings were located in lodgepole pine forest types 35% of the time (as well as 20% within subalpine fir forest type, 23% in Engelmann spruce/subalpine fir forest type, 6% in Douglas-fir forest type, and <1% in other forest type), compared to only 16% of the time within whitebark pine forest types, and thus regeneration location is not just dependent on an overstory of mature whitebark pine or a whitebark pine forest type (Goeking, Izlar et al. 2018). There are also studies that show potential for increased whitebark pine regeneration following a disturbance, such as white pine blister rust or mountain pine beetle attacks, as the resulting mortality opens up gaps in stands with denser canopies (Larson and Kipfmüller 2010, Meyer, Bulaon et al. 2016). Many of the sites sampled for this study were considered to be mixed-conifer stands. Despite the lack of a dominant overstory canopy of mature whitebark pine or disturbance that would encourage seed caching from Clark's nutcrackers, the results demonstrate that in undisturbed stands with even limited seed sources, whitebark pine continue to establish, in agreement with several recent studies (Clason, Macdonald et al. 2014, Goeking and Izlar 2018). The establishment date data showed that while 51% of the subsampled whitebark pine regeneration above 6 inches in height were older than 50 years, that many of them were more recently established, and not just suppressed due to abiotic stress. Whitebark pines' slow growth patterns can make for uncertainty in age

classes of recorded regeneration numbers, but the results for this study demonstrate continuing establishment of whitebark pine rather than a height suppressed population. Goeking and Izlar et al, 2018, used data from 1,217 FIA (Forest Inventory and Analysis plots) to assess whitebark pine seedlings densities throughout the US Rocky Mountains. They found that despite 83% of the sites where whitebark pine seedlings occurred being in non-whitebark pine forest types that densities were frequently higher in whitebark pine forests. However, the highest density (6,447/acre) of whitebark pine seedlings did occur within a lodgepole pine forest type. These results contrasted with my findings in which the highest whitebark pine seedling densities were found in whitebark pine/subalpine fir forest types(Goeking, Izlar et al. 2018). The same study, using FIA plot data from all stand types, not just those with a whitebark pine component, found that out of 7,018 FIA plots included in the analysis, 1,217 (17%) had whitebark presence and 795 (11%) had whitebark pine seedlings present (Goeking, Izlar et al. 2018). Despite the high numbers of subalpine fir seedlings recorded in this study, given their lack of fire resistance and nutrient availability needs, as well as simple space demands, it is not possible for them to grow to maturity in the high density they stock themselves as seedlings. A study in Colorado, taking place from 1961-1975, showed that as many as 14 one-year old subalpine fir seedlings were required to have one seedling that survived till at least 4-13 years of age (7% survival rate) (Noble and Ronco Jr 1978, Alexander, Shearer et al. 1990). While there are no published studies on long term seedling survival of whitebark pine in a naturally planted setting, intentionally planted seedlings were found to have a survival rate over a eleven year period ranging from 2-47%, dependent on the physiographic location of the site, with other datasets showing up to an 86% survival rate on dry sites near Cooke City, Montana (Scott and McCaughey 2006). While the age of every recorded seedling is unknown within this study, when comparing the average

sampled density of whitebark pine seedlings (1,054 per acre) to mature density (187 per acre), the seedling survival rate for these minimally disturbed stands would need to be 5.6% to replace the mature.

Interseries correlations in dendrochronology represent the similarity in long-term growth patterns between a sampled core or tree and the associated ring width data when compared to other sampled trees within the selected region. Yearly radial growth and growth patterns are a product of the environment and climate a tree exists in. Ring width data can be used to recreate past climates and fire history events, and higher interseries correlations allow for greater confidence in climate and corresponding radial growth interpretations (Fritts 1976, Fritts and Swetnam 1989). While sites used within this study were located throughout the range of Northern Rockies whitebark pine habitat, radial growth patterns from sites that are located near the outside edge of a species' ecological niche frequently have higher correlations with climate data. The outer edges of habitats exist as a result of the limiting factors of moisture or temperature stress, and radial growth patterns become more variable as a result of this stress, which then results in higher correlations to the limiting climate variable. Interseries correlation levels differ by species, size of sampled area, site disturbance history, and homogeneity of area sampled. While the 1/10<sup>th</sup> acre plots used in this study had minimal disturbance, many still had low interseries correlations (considered to be <0.3). The sites with low interseries correlations are likely the result of very pale, narrow or missing rings (as can occur under severe abiotic stress), broken cores with missing sections, sample depth, or simply a divergent population. Other studies of high elevation conifer species have also found low interseries correlations ( $RWI_{site}$ ) when correlating ring widths by site. These studies also showed positive correlations with winter and spring precipitation and negative correlations with spring to summer

temperatures, although the correlation values of those studies are stronger than some of the correlation values of this study (Perkins and Swetnam 1996, Frank and Esper 2005, Kipfmüller and Salzer 2010, Dolanc, Westfall et al. 2013). The lower climate correlation values found in this study are attributed to the large region sampled (northern Rocky Mountains), the range of habitat types and biophysical site characteristics, and correlating ring width growth ( $RWI_{\text{region}}$ ) with individual months rather than seasonally. The coarse climate data used (each grid cell covering of 16 square kilometers) likely led to lower correlations with the monthly climate data, as within such a large area, climate and site characteristics can range greatly across topographically dynamic regions. The sites used within the study for the RWI and climate correlation work had interseries correlations ranging from 0.3-0.73, although the sites with higher interseries correlations had lower numbers of cores used. However, there are study results showing that same species chronologies are not necessarily similar in their response to climate and one species site chronology should not be expected to have the same response as another spatially distinct group of the same species (Schuster and Oberhuber 2013, Salzer, Larson et al. 2014, Shrestha, Chhetri et al. 2017, Holz, Hart et al. 2018). Studies have shown that conifer species are limited by different variables within their location within their habitat. Given similar spatial area and site characteristics, trees lower along the elevational gradient of their habitat are often limited by moisture, while the trees at the higher elevations are more limited by growing season temperatures (King, Gugerli et al. 2013, Salzer, Larson et al. 2014, Shrestha, Chhetri et al. 2017, Liu, Liang et al. 2018). Differing elevation and aspect, and therefore climate and microsite variation, are the most common contrasts when the same species provide differing responses and limitations to climate, suggesting that future predictions for species should be made considering niche locations as much as regional or climate based predictions (Peterson and Peterson 1994,

Hughes and Funkhouser 2003, Kipfmueller and Salzer 2010, Carrer 2011, van de Gevel, Larson et al. 2017).

Climate projections for the Northern Rockies for the next hundred years suggest an increase in mean annual temperatures from 3.6 to 7.2 °F (Running 2008). Having available moisture during the summer months ensures that whitebark pine can keep growing, rather than close their stomatal openings and shut down growth due to drought stress. It also allows the tree to develop next year's buds within the stems and produce sugars and proteins that will be used in the next few years of the trees life. Whitebark pine depend on lingering snowpack and moist soils to do such, but the warming temperatures and decreasing annual precipitation suggested by Figure 9 from this study, as well as from other published studies, could affect both variables (Pederson, Graumlich et al. 2010, Pederson, Gray et al. 2011, Pederson, Betancourt et al. 2013). Despite this, the data from this study do not show greatly modified growth, although certainly climate growth-response thresholds may be reached with increasing drought stress in the future. While the ring-width growth patterns do correlate most strongly with growing season precipitation variations, whitebark pines' continued growth in these sampled sites suggest that they may be responding to other unmeasured factors, such as CO<sub>2</sub> fertilization or the increase in growing degree days associated with steadily warming temperatures. Continuing drought stress may also affect the other species found on the sites first, such as subalpine fir, as they are much less drought-tolerant and often rely on whitebark pine to establish and to act as shade for their encroachment.

Results from other studies focusing on high-elevation conifer species radial growth to climate change are mixed. Within the United States, bristlecone pine (*Pinus aristata* Engelmann and *Pinus longaeva* D.K. Bailey) are frequently used for dendrochronology work due to their

long lifespans. Recent studies involving them have found both unprecedented growth within their upper elevational band (Salzer, Hughes et al. 2009), to both a lack of a trend or a negative trend in growth (Kipfmueller and Salzer 2010). Kipfmueller and Salzer, 2010, compared 66 five-needle pine chronologies from 1896 to the end of their individual records and found that 42% of them had a significant positive growth trend, while 23% had a significant negative growth trend, and 35% showed no significant trend at all. This same study showed that 65% of the chronologies exhibiting significant positive trends were located near treeline. However, whitebark pine represented 47% of the chronologies with significant negative trends in radial growth (Kipfmueller and Salzer 2010). Other studies focusing on upper elevation tree species, however, show a steady increase in radial growth over time (Rolland, Petitcolas et al. 1998, Dolanc, Westfall et al. 2013). However, changing growth-climate responses are also leading some scientists to hypothesize that climate-response thresholds are varying within species as well as spatially as predictions based on growth-climate response outcomes are not capturing the actual responses (Andreu, Gutierrez et al. 2007, Oberhuber, Kofler et al. 2008, Fajardo and McIntire 2012, Salzer, Larson et al. 2014) .

## **5 Conclusions**

Minimally disturbed stands with a mature whitebark pine component can still be found throughout the US Rocky Mountains. Within the sites sampled in this study, whitebark pine populations still averaged 25% standing dead. While this is much lower than the overall US Rocky Mountains averaged standing dead percentage of 51%, it is still higher than the standing dead rate for the other conifer species within these sampled stands, which only averaged 16%. However, the whitebark pine seedling and sapling density and establishment data from this study showed that

within these stands there is continuing regeneration. While densities of seedling and sapling whitebark pine are frequently lower than subalpine fir in stands that contain both species, predictions for increased fire on the landscape may help eradicate the competition species. As well, ring width index data from the mature whitebark pine did not show an overall change over the 100 years sampled, even though the monthly climate variables with the highest correlation coefficients are mostly showing hotter and drier trends, which should have a negative effect on radial growth. The fact that there has not been a pronounced change in ring width growth allows for the hypothesis of increased growing degree days or another unmeasured variable potentially making up for the predicted loss of growth from drought stress. The continuing radial growth and regeneration of whitebark pine among the sampled sites, despite their broad differences in both spatial and biophysical characteristics, implies there may be room for interpretation of negative predictions of future whitebark pine presence and growth. While white pine blister rust and mountain pine beetle are still a formidable presence on the landscape, there may still be the potential for successful re-establishment by managers under the current climate conditions.

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**A.**

Mtn. Range	State	Site ID	Dominant Species (if > 10%)			Site Descriptors		% Whitebark Presence		% Other Conifer Species	
			Canopy	Sub-Canopy	Understory	Elevation	Aspect	Live	Dead	Live	Dead
Absaroka	MT	33	PIAL	ABLA	VASC	9090	86	35	41	0	24
Absaroka	MT	34	PIAL	PIAL	VASC	9655	216	0	50	0	50
Absaroka	MT	35	PIAL	PIAL	VASC	9125	80	6	50	6	38
Anaconda	MT	86	PIAL	ABLA	VASC	8171	262	0	66	0	34
Anaconda	MT	92	PIAL	ABLA	VASC	8329	39	0	60	0	40
Beartooth	MT	29	ABLA	ABLA	VASC	8943	150	0	79	0	21
Beartooth	MT	30	PIAL	PIAL	POCU	9708	230	0	70	0	30
Beartooth	MT	31	ABLA	ABLA	ARCO	9175	220	8	19	0	73
Beartooth	ID	32	PIAL	PIAL	ARCO	10090	260	3	97	0	0
Beaverhead	MT	18	PIAL	PIAL	ARLA	8896	82	0	22	25	53
Beaverhead	MT	19	PIAL	PIAL	CARU	8982	117	0	100	0	0
Beaverhead	MT	20	PIAL	PIAL	LUSE	8521	160	0	74	9	17
Beaverhead	MT	21	PICO	PIAL	VASC	8570	130	0	30	3	67
Beaverhead	MT	39	PIAL	PICO	VASC	7929	256	6	20	20	54
Beaverhead	MT	40	PIAL	PIAL	XETE	8519	110	0	100	0	0
Beaverhead	MT	41	PIAL	ABLA	XETE	8425	4	3	47	0	50
Beaverhead	MT	42	PIAL	ABLA	XETE	8540	110	14	52	5	29
Beaverhead	MT	85	PIAL	PIAL	FEID	9022	284	30	70	0	0
Beaverhead	MT	93	PIAL	PIAL	FEID	8879	86	0	100	0	0
Beaverhead	MT	94	PIAL	PIAL	FEID	8995	117	11	89	0	0
Bitterroots	MT	1	PIAL	MEFE	MEFE	6347	264	7	34	3	55
Bitterroots	MT	27	PIAL	PIAL	CAGE	8359	162	16	79	0	5
Bitterroots	MT	28	PICO	ABLA	XETE	8249	280	3	19	0	77
Bitterroots	MT	36	PIAL	PIAL	CAGE	8271	212	24	55	0	21
Bitterroots	MT	37	PICO	ABLA	VASC	8038	242	10	17	5	69
Bitterroots	MT	38	PIAL	ABLA	VASC	7999	84	8	48	8	36
Bitterroots	MT	51	PIAL	PIAL	XETE/VASC	7985	112	33	42	3	21
Bitterroots	MT	54	PIAL	ABLA	VASC/XETE	7155	80	28	30	5	37
Bitterroots	MT	65	PICO		VASC/VAGL	6769	175	2	12	0	86
Crazy	MT	61	PIAL		VASC	8356	320	33	64	0	3
Flathead	MT	2	ABLA		XETE	6742	188	29	29	0	43
Flint Creek	MT	74	PICO	ABLA	VASC	7842	210	2	41	10	46
Flint Creek	MT	87	PIAL	ABLA	VASC	8171	262	14	25	7	54
Gallatin	MT	55	ABLA		VASC	7950	50	35	13	2	51
Gallatin	MT	56	PICO		VASC	8519	205	25	40	4	31
Gravelly	MT	6	PIAL		FEID	8653	220	16	84	0	0
Gravelly	MT	8	PIAL		ARTR	8294	258	0	100	0	0
Gravelly	MT	9	PIAL		TAOF	8164	346	5	60	0	35
Gravelly	MT	10	PIAL	PIAL	ACME	9290	358	20	80	0	0
Gravelly	MT	11	PIAL	ABLA	CHAN	8373	82	50	17	6	28
Gravelly	ID	83	PIAL		FESTUCA	8692	178	7	93	0	0
Little Belt	MT	62	PIAL		VETCH/GAB	7956	280	12	87	0	2
Little Belt	MT	63	PIAL		LUAR/GABC	7235	180	0	100	0	0
Little Belt	MT	64	PIAL		VASC	8198	280	54	43	0	2
Madison	MT	57	PIAL		THOC	8482	120	0	38	0	63
Madison	MT	58	PIAL		ARLA/CARU	9080	300	63	36	0	1
Madison	MT	59	PIAL		GEVE/CAGE	8255	210	5	95	0	0
Madison	MT	60	PICO		THOC/SYAL	8052	240	24	40	12	24
Pioneer	MT	43	PICO	PIAL	VASC	8109	320	0	19	9	72
Pioneer	MT	44	PIAL		VASC	8564	60	21	28	0	52
Pioneer	MT	45	PIAL		VASC	9124	248	22	78	0	0
Pioneer	MT	46	PIAL		FEID	8263	246	0	83	0	17
Salmon River	ID	22	PIAL	ABLA	ABLA	8934	358	3	30	19	48
Salmon River	ID	23	PIAL	PIAL	VASC	9301	250	37	47	0	16
Salmon River	ID	24	PIAL	ABLA	VASC	8617	350	6	14	17	63
Salmon River	ID	25	ABLA	ABLA	CARU	8736	290	2	19	15	65

Sapphire	MT	52	PIAL	ABLA	VAGL	7329	290	0	26	11	63
Sapphire	MT	53	ABLA	ABLA	XETE	7393	310	4	20	0	76
Sapphire	MT	88	PIAL	ABLA	VASC	7958	148	8	25	20	48
Sawtooth	ID	26	PIAL	ABLA	CAGE	8846	260	26	39	13	23
Sawtooth	ID	66	PIAL	PIAL	CAGE	9302	180	15	78	0	7
Sawtooth	ID	67	PIAL	PIAL	FEID	9386	170	33	67	0	0
Sawtooth	ID	68	PIAL	PIAL	Antennaria	9485	16	0	100	0	0
Sawtooth	ID	69	PIAL	PIAL	CAGE	9381	90	14	86	0	0
Sawtooth	ID	70	PIAL	PIAL	ARTR/CAGE	9192	140	0	100	0	0
Sawtooth	ID	71	PIAL		ARTR/FEID	8300	220	0	91	0	9
Sawtooth	ID	72	PIAL	ABLA	CAGE/LUSE	9221	200	0	82	0	18
Sawtooth	ID	73	PIAL		CAGE	9237	180	0	67	13	20
Sawtooth	ID	90	PIAL	ABLA	VASC	8543	12	0	33	0	67
Snowcrest	MT	91	PIAL		ARTR	8348	200	8	92	0	0
Swan	MT	3	ABLA	MEFE	MEFE	6436	280	21	13	13	54
Swan	MT	4	ABLA	MEFE	MEFE	6342	328	18	12	18	53
Swan	MT	5	PICO	ABLA	VAGL	6580	200				
Swan	MT	7	PSME	PSME	VAGL	6827	180	0	20	0	80
Swan	MT	47	ABLA	ABLA	XETE	7518	88	13	20	13	53
Swan	MT	48	PIAL	ABLA	XETE	7308	240	50	12	0	38
Swan	MT	49	PIAL	ABLA	VASC	7332	37	19	31	19	31
Tobacco Root	MT	12	PIAL	ABLA	ARLA	8892	120	0	39	3	58
Tobacco Root	MT	13	PIAL	ABLA	ARLA	8573	116	44	40	4	12
Tobacco Root	MT	14	PIAL	ABLA	FEID	8431	116	25	75	0	0
Tobacco Root	MT	15	PIAL	PIAL	PIAL	8056	218	55	38	0	7
Tobacco Root	MT	16	PIAL	ABLA	VASC	8825	130	0	59	2	39
Tobacco Root	MT	17	ABLA	ABLA	VASC	8398	62	0	14	7	79
Wind River	WY	50	PICO	ABLA	VASC	8515	240	21	21	12	45
Wind River	WY	75	PIAL	POTR		6992	144	2	32	9	57
Wind River	WY	76	PIAL	PIAL	RIBES	8189	246	10	44	10	37
Wind River	WY	77	PIAL	PIAL	ARTR	8252	246	0	90	0	10
Wind River	WY	78	PIAL	PIAL		9372	18	6	88	0	6
Wind River	WY	79	PIAL			9386	26	0	100	0	0
Wind River	WY	80	PIAL			9678	337	9	87	0	4
Wind River	WY	81	PIAL		ARTR	9519	262	15	85	0	0
Wind River	WY	82	PIAL			8972	222	5	42	16	37

Table A1: From left to right, mountain range that site is located within, identifying plot number, dominant canopy species, dominant sub-canopy species, dominant understory species, elevation at site, aspect, percent dead whitebark, percent live whitebark, percent dead all other conifer species, and percent live all other conifer species. Data extends only to area sampled, and for a species to be considered dominant, it must have at least 10% cover on the plot.