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GROWTH RESPONSE OF WHITEBARK PINE *(PINUS ALBICAULIS)* REGENERATION TO

THINNING AND PRESCRIBED BURN RELEASE TREATMENTS

By

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Growth response of Whitebark pine *(Pinus albicaulis)* regeneration to thinning and prescribed burn release treatments

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Abstract: Whitebark pine (*Pinus albicaulis* Engelm.) plays a prominent role throughout high-elevation ecosystems in the northern Rocky Mountains. It is an important food source for many birds and mammals, as well as a major player in high-elevation watershed maintenance, both slowing snowmelt and stabilizing soils. Whitebark pine is vanishing from the landscape due to three main factors – white pine blister rust (*Cronartium ribicola*) invasions, mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, and successional replacement by more shade-tolerant tree species historically controlled by wildfire. In the past century, human activity such as fire suppression has altered these systems, potentially causing dramatic changes to the landscape. Managers now are implementing a variety of treatments across the landscape to encourage whitebark pine regeneration and survival. The objective of this study was to determine how whitebark pine regeneration (less than 9 inches diameter at breast height) responds to selective thinning and prescribed burn treatments, otherwise known as release treatments, intended to cause an increase in annual growth. I examined the growth ratio (GR) obtained from tree cores and destructive sampling at four sites in Montana and Idaho treated in the late 1990s. Overall, the average annual radial growth rates of the trees in treated areas was greater than that of trees in control areas. Specifically, there were significant increases in the GR in the two sites that were both thinned and later burned. All sites showed high variability in the GR of individual trees; however, there was greater variability in the annual growth rates of trees in treated areas than in trees from the control areas. I also mapped the height to age relationship of a subsample of the trees to examine how the vertical growth profile changed after treatment. Results suggest that whitebark pine regeneration can respond to thin and burn release treatments and that managers may see positive results in other areas that are treated similarly.

Key Words: Whitebark pine, regeneration, release treatments, restoration

Acknowledgement:

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Introduction

Landscapes are constantly in flux, forcing species within them to keep pace with ever-changing conditions. Over centuries, weather patterns and disturbance regimes vary, invading species encroach, and plants are exposed to new diseases (Ellison et al. 2005). Native species struggle to cope with and adapt to these many changes (Liu et al. 2016). Adaptability of a species to change greatly affects its ability to survive. Species experiencing multiple disturbances at the same time have a greater risk of suffering a population-wide decline, depending upon that species' adaptive capacity (Ellison et al. 2005). Whitebark pine (*Pinus albicaulis* Engelm.) is one such species with multiple disturbances acting upon it (Keane et al. 2007).

Whitebark pine is a foundation species throughout high elevation forests of the western United States and Canada (Ellison et al. 2005, Tomback and Achuff 2010). This tree serves as a foundation species by promoting biodiversity throughout high elevation ranges and by stabilizing ecosystem functions such as water quality and quantity regulation (Ellison et al. 2005, Keane and Parsons 2010, Tomback and Achuff 2010). Whitebark pine is a long-lived, slow-growing tree with moderate shade tolerance (Minore 1979, Eggers 1990). It can easily reach 400 years in age; the oldest tree ever recorded was more than 1300 years old (Arno and Hoff 1990). In the northern portions of its range, whitebark pine is usually replaced by more shade-tolerant species such as subalpine fir (*Abies lasiocarpa* Hook), Engelmann spruce (*Picea engelmannii* Engelm)*,* and mountain hemlock (*Tsuga mertensiana* Bong) (Keane and Parsons 2010). These shade-tolerant species replace whitebark pine in the overstory 50 to 250 years after a stand replacing disturbance, depending on the previous fire history and local environments (Arno and Weaver 1990, Keane 2001).

Whitebark pine has the most extensive distribution of all the five-needle pines, occurring at high elevations in seven U.S. states and two Canadian providences (Tomback and Achuff 2010). Whitebark is found throughout the Rocky Mountains of Wyoming, Idaho, Montana, Alberta, and British Columbia, as well as in the Sierra Nevada and Cascade mountains in California and the Pacific Northwest. Small populations occur sporadically in the Great Basin of Nevada, and in the mountains of northeast Oregon and Washington (Keane et al. 2012). Whitebark pine communities comprise up to 15% of the forested areas throughout the Rocky Mountains (Arno 1986) with the majority of populations occurring on public lands, including wilderness areas, national parks, and national forests. The three largest wilderness areas in the contiguous U.S. - the Bob Marshall Wilderness Complex, the Selway-Bitterroot-Frank Church Wilderness Complex, and Yellowstone National Park - each contain about 25 to 50% potential whitebark pine forest habitat (Keane 2000). Whitebark pine typically grows either as a seral species, eventually being replaced by more shade tolerant species, or as a climax species in climates too inhospitable for other conifer species to thrive (Arno and Hoff 1989).

Whitebark pine is an important food source for around 110 animal species (Kendall 1980). Its large seeds are depended upon by many creatures including black bears (*Ursus americanus* Pallas), grizzly bears (*Ursus arctos horribilis* Linnaeus), red squirrels (*Tamiasciurus hudsonicus* Erxleben) (Kendall 1980), and most importantly, Clark's nutcrackers (*Nucifraga columbiana* Wilson) (Tomback 1982). Whitebark pine has a mutualistic relationship with the nutcracker, relying on the bird to disperse its heavy, wingless seeds (Tomback 1982). The nutcracker-stonepine interactions are regarded as coevolved mutualisms where the three species of nutcrackers worldwide are the primary seed dispersers for the five species of stone pines (trees that retain the mature seed within the cone; Hutchins and Lanner 1982). The Clark's nutcracker harvests seeds from the whitebark

pine cones and transports them to a cache up to 10 km away from the parent tree (Lorenz et al. 2008). Nutcrackers often cache their seeds in large open areas, usually old burns, with plenty of visual markers to help the birds relocate their cache. However, some of these caches are forgotten and the seeds later germinate (Tomback 1982, Arno and Hoff 1990).

Whitebark pine is generally the first species to reestablish in an area that has experienced a stand-replacing fire, thanks to its relationship with the Clark's nutcracker and specific physiological traits, such as its ability to tolerate drought (Leirfallom et al. 2015). The traits may then help the tree facilitate the establishment of other conifer species, particularly subalpine fir and Engelmann spruce (Callaway 1998, Resler and Tomback 2008). A study done by Sala et al. (2001) comparing the instantaneous gas exchange and water use efficiency between mature subalpine fir and whitebark pine trees found that whitebark pine use water more efficiently. This trait allows whitebark pine to colonize much dryer sites and act as a nurse plant for less drought-tolerant species. It also reinforces the importance of whitebark pine to high-elevation communities.

Invasive fungal pathogen, native insects, and successional replacement by more shade-tolerant species are important ecosystem drivers that have sent whitebark pine into a tailspin of decline. White pine blister rust (*Cronartium ribicola* Fischer*)* is an exotic pathogen that attacks most five-needle pines, but is particularly deadly to whitebark pine (Bingham 1972, Hoff et al. 1980, Arno and Hoff 1989). This disease was introduced into North America around 1900 on Eastern white pine (*Pinus strobus* Martínez) seedlings grown in European nurseries (Maloy 1997). By the 1950's, white pine blister rust was widespread throughout most of North America (McKinny and Tomback 2007). White pine blister rust is currently present throughout most of the range of whitebark pine, reducing cone production and killing trees (Schwandt et al. 2010,

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Tomback and Achuff 2010). White pine blister rust requires two hosts, a five-needle pine and most commonly a species from the *Ribes* L. family such as a currant (e.g., *Ribes lacustre* Poir; found throughout the study region). Blister rust spores grow through the stomatal openings in the needles of the pine. The infected area of the tree swells and forms blisters which rupture and release bright orange aeciospores in the spring. These spores infect the alternate host which produces basidospores in the fall that can infect more trees (Maloy 1997).There is variation in the estimated levels of white pine blister rust, but likely levels range from 0-24% in the Sierra Nevada Range (Maloney 2011) to as high as 73% in the Rocky Mountains (Smith et al. 2008). In Waterton Lakes National Park, Alberta, Smith et al. (2008) reported stands last assessed in 1996 showed increases in infection levels from 43% to 71%, and also observed that mortality increased from 26% to 61%. Although tree mortality may not occur for decades, infected trees rapidly lose the ability to produce cones (McKinny and Tomback 2007) thus reducing the likelihood of regeneration.

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins*)* is an aggressive insect, native to western North America, that attacks most pine trees (Wood 1982). These insects play an important role in the life of a forest, attacking and killing old or weakened trees, thus accelerating development of understory cohorts by increasing their access to nutrients, light, and water (Hansen 2014). Mountain pine beetles create breeding chambers in the living wood and lay eggs under the bark. The beetles introduce blue stain fungi into the sapwood, which reduces the trees' ability to repel attacking beetles with pitch. The joint action of larval feeding and fungal colonization kills the host tree within a few weeks of a successful attack, as these two processes interrupt water transport and girdle the tree by cutting off the flow of water and nutrients (Dooley et al. 2015). Several major mountain pine beetle outbreaks over the last 90 years have killed many mature cone-

bearing whitebark pine across the range (Logan and Powell 2001). Current climate-facilitated severe outbreaks have additionally reduced the numbers of large, cone-bearing, whitebark pine, severely depressing the regeneration potential of the species (Logan and Powell 2001, Schwandt et al. 2010, Macfarlane et al. 2013).

Finally, the large-scale suppression of wildfires over the last 100 years has led to successional replacement of whitebark pine by more shade-tolerant species including subalpine fir and Engelmann spruce (Arno 1986, Keane et al. 1994, Murray et al. 2000). These species replace whitebark pine in the overstory 50 to 250 years post-fire depending on the previous fire history and local environments (Arno and Weaver 1990, Keane 2001). Whitebark pine stands typically experience three distinct types of fire regimes: mixed-severity, low-intensity, and stand-replacing. The most common fire regime is a mixed-severity regime where the fire varies in intensity and frequency, creating patchy mosaics of mortality and survival across the landscape (Morgan et al. 1994). Mixed-severity fires generally occur every 60-300 years and are usually less than 50 hectares in size (Arno and Weaver 1990). These mix-severity burns include areas of non-lethal underburns and areas of stand replacing fire (Morgan et al. 1994).

Whitebark pine is physiologically better equipped to survive such fires than other high-elevation species due to its thicker bark, deeper roots and thinner crowns (Morgan et al. 1994). In areas with sparse surface fuels, these fires typically are low-intensity ground fires that kill only young, thin barked trees and rarely damage mature trees. Increased fuel loads or high winds can increase the severity of the fire (Arno and Hoff 1990, Morgan et al. 1994). Some whitebark stands only experience light underburns due to consistently low fuel loads, such as those found in the most southern parts of the tree's range (Morgan et al. 1994). However, the majority of whitebark pine stands in the species' northern range establish after large stand-replacing fires occur and

Clark's Nutcrackers cache seeds in the newly burned areas (Murray et al. 2000). With continued exclusion and fire suppression, these large, stand-replacing fires are occurring less frequently.

The combination of these three factors, white pine blister rust, mountain pine beetle, and fire exclusion, have contributed to a nearly range-wide decline in whitebark pine populations; as a result, it was recently listed as both a candidate species under the United States Endangered Species Act (US Fish and Wildlife Service 2011) and an endangered species in Canada under the Species at Risk Act (Government of Canada 2012).

Whitebark pine is highly dependent upon the Clark's nutcracker for successful regeneration (Tomback 1982). As populations of whitebark continue to decline, the bird may revert to seed predation, consuming more whitebark pine seeds than it caches (Schaming 2015). Furthermore, with the exclusion of fire from the landscape, forest openings that Clark's nutcrackers favor for caching seeds are becoming sparser as they are overgrown with shade-tolerant fir and spruce. These shade-tolerant species out-compete existing whitebark pine seedlings (Arno and Hoff 1989). This reduces the chances that the seedlings will eventually become cone-producing adults. As these openings dwindle, so do the chances that any genetic resistance to blister rust will be passed on since it is unlikely resistant seedlings will mature and produce cones under such heavy competition (Keane et al. 2000).

Restoration in whitebark pine ecosystems is challenging and costly. Therefore, it is important for managers to understand the most effective restoration methods in order for the most beneficial and cost effective decisions to be made. The physical environment of high-elevation ecosystems is subject to severe temperature swings, poor quality soil, high winds, and a lack of soil moisture in the summer months (Arno and Hoff 1989). However, extensive research and modeling predict that without successful restoration activities whitebark pine populations will

continue to decline, potentially changing high elevation landscapes throughout the west (Keane et al. 2000).

Little research has been done examining the success of currently used restoration methods. At the moment, the most effective methods are believed to be selective cuttings which focus on removing shade-tolerant species, and prescribed burns which remove slash and kill seedlings, creating openings for nutcrackers to cache cones (Keane et al. 2000). Both of these methods attempt to create an environment suitable for increasing whitebark pine radial growth rate. Release treatments are commonly defined as a variety of treatments designed to free young trees from undesirable, usually overtopping, competing vegetation (Silviculture Instructors Subgroup 1994, Brockwell and Davis 2002). For this study, I evaluated growth release primarily as an increase in annual radial growth, and release treatments as the selective thinning and prescribed burns conducted on the study sites.

Study Objective

This study builds upon previous work done by Keane et al. (2007) which examined the diameter growth response of whitebark pine greater than 23 cm in diameter at breast height (DBH; 1.37 m) to the removal of competition through harvest. Results from that study showed that larger whitebark pine responded well to release treatments, showing an increase in annual radial growth in the years following treatment (Keane et al. 2007). However, there are very few data to determine if the same release methods also work on whitebark pine regeneration. Keane et al. (2007) were unable to analyze data from young trees because they did not contain enough growth rings prior to harvest to calibrate their gorwth models. The main objective of this study was to examine the basal area increment of whitebark pine regeneration (defined as less than 23

cm DBH) to release treatments, focusing specifically on the trees' growth ten years pre-treatment and their response ten years post-treatment.

During the summers of 2016 and 2017, I sampled 90 trees from four sites that received combinations of selective thinning and prescribed burning in the late 1990s and early 2000s. Each site was paired with a corresponding control that was also sampled to establish a baseline of tree growth. I hypothesized that whitebark pine regeneration in treated units would display an increase in annual radial growth post-treatment, while little or no release would occur in the control sites; this would result from the reduction in competition and increase in available resources imparted by the treatments. In addition, I evaluated site conditions within the treatment areas that may have influenced whitebark pine radial growth response. I also graphically examined the height growth response of the trees to the treatments.

Methods

Study Sites

I selected four sites in the Northern U.S. Rocky Mountains (Bear Overlook, Beaver Ridge, Coyote Meadows, and Snow Bowl) which were part of the Keane et al. (2010) long-term monitoring study examining whitebark pine restoration through selective thinning and prescribed burnings. The four sites were treated in 1999-2001 (Table 1). Pre-treatment measurements were taken in the mid-1990's in monitoring plots, and they were re-measured 1-year post-treatment and then every five years for fifteen years. Regeneration sample trees were drawn from the same sites as these monitoring plots, but not from within those plots. I used the monitoring plot data to determine the pre- and post-treatment conditions across the sites but located distinct sample plots within each. Of the sites, three are located in Montana, and one in Idaho (Figure 1). They range in elevation from 2088 m to 2438 m and have southerly aspects (Table 1).

Multiple treatment and control units were laid out at each site when the monitoring plots were established in the 1990's. Each unit was thinned, burned, received a mix of both treatments, or was left untreated as a control. In the thinned units, three competitive species were removed: the subalpine fire, Engelmann spruce, and mountain hemlock. Lodgepole pine (*Pinus contorta* Douglas ex Loudon) was not removed because the investigators in charge of the original study did not think that its density negatively impacted whitebark survival (Keane et al. 2007). In burn-only units, prescribed fires were mostly lit by hand with drip torches, though Beaver Ridge units were burned with a flame thrower mounted on a truck (Keane and Parsons 2010) Fires were allowed to burn freely, resulting in a mixed-severity fire with unburned areas intermixed with burned patches. The thin-burn units were first thinned to remove competitive species and then broadcast burned to dispose of the slash. These units burned more evenly due to the connectedness of the unpiled fuels (Keane and Parsons 2010).

The Snow Bowl, Bear Overlook, and Coyote Meadows sites were all thinned, albeit to and from different initial densities. Thinning was the only treatment conducted at the Snow Bowl site. Bear Overlook and Coyote Meadows both received prescribed burns in the thinning units. Coyote Meadows also had some units that were only burned (Table 1). At Beaver Ridge, 0.08 to 2 hectare burn-only units were created to encourage nutcracker caching (Keane and Parsons 2010). Thin-only and thin-burn units were also established at Beaver Ridge. However, many of them burned completely when a wildfire swept through the area in 2002 and were not sampled for this study. The burn-only units and their control unit at Beaver Ridge did not burn. The monitoring plots were re-measured intermittently (approx. every 5 years) to assess re-establishment of tree species, particularly whitebark.

Field Sampling Methods

Sample locations within each treatment unit at a given study area were selected at random from a grid of points overlaid on the unit and located with a recreational-grade global positioning system (GPS) unit. Once the plot center was located by the field crew, a fixed area 11.3 m radius plot was established (Figure 2). North and east photos were taken from plot center to provide a visual description of the plot. A hemispherical lens was also used to take an upward photo to later use for calculating the tree canopy cover on the plot. The FFI methods (FEAT (Fire Ecology Assessment Tool) and FIREMON (Fire Effects Monitoring and Inventory Protocol) integration system, Lutes et al. 2009) for measuring plot and tree characteristics were used to collect plot specific information. I recorded universal transverse Mercator (UTM) coordinates for each plot, plus elevation (m), landform, aspect, slope, ground cover, and habitat type (Arno and Hoff 1989). The height, DBH, and health status (healthy, unhealthy, sick, dead) of all trees (> 11.4 cm DBH) within the plot boundary was also collected. The DBH of the trees was later used to calculate the aggregate basal area of the plot. The same information was collected for all of the saplings on the plot (trees < 11.4 cm DBH). A dot tally by species and height was done for the seedlings (trees < 1.4 m in height) on an additional nested fixed area plot with a radius of 2 m.

I selected sample trees based on the health and vigor classes adapted from Keen's (1943) ponderosa pine classifications. Changes were made to the original tree classes to better fit the morphology of whitebark pine with guidance from Kipfer (1992) (Table 2). No more than four whitebark were sampled on each plot. The sample trees were selected through a combination of diameters and health/vigor ratings to ensure that no particular size class or vigor group was favored (Tables 3 and 4).

A sample tree was first photographed from the north and east to capture the tree's shape and growth form. The total height and DBH of the tree was collected and the tree was also described using the terms in Table 3 and given a health and vigor rating. If the tree was large enough (usually >5 cm DBH) then a core was taken from the base of the tree, perpendicular to the slope, and a second at breast height. Cores were placed in paper straws for storage and transport. Each straw was labeled with the plot number, sample tree number, and core number. Trees too small to core successfully were cut down with a hand saw at the base of the tree, and five sections (discs) of the tree were removed, one from the base and the other 4 at evenly spaced intervals up the tree. Each section was labeled with the plot number, tree number, and section number, and packaged up for transport back to the lab.

Laboratory Procedures

All of the field data was entered into the appropriate FFI databases. The individual photos of the trees from each plot were labeled with the plot number, tree number, photo direction (north, east) and stored in a specific photo project file. Cores and tree sections were sanded with a belt sander and hand-polished with 9 micron grit sandpaper, then scanned using an Epson platform scanner at 1200 dpi. If the tree rings were hard to discern at this resolution, a slice of the specimen was removed using a rotary microtome, stained with a blend of Safranin and Astrablue dye, mounted on a slide, and rescanned (Figure 3). I used CooRecorder 7.8 (Cybis 2015) to date and measure annual radial growth. The program CDendro (Cybis 2015) was then used to crossdate the samples and create a chronology for each site (site specific series intercorrelation =0.35-0.4; mean sensitivity =0.3).

Data Analysis

I used the dplR package (Bunn 2008) in RStudio 3.3.2 (R Core Team) to calculate basal area

increments (BAI; mm² yr^{-1}) at the base of the tree (not breast-height) for each individual tree. I

used these measurements to create growth ratios (GR) for each tree, relating growth post-treatment

to growth pre-treatment. Growth ratios greater than 1 translate to an increase in growth by the tree,

and growth ratios less than one equate to a decrease in growth. GR was calculated by dividing the

post-treatment 10-year BAI (BAI_{+10}) by the 10-year pre-treatment BAI (BAI_{-10}):

Equation 1: $$GR = \frac{BAI_{+10}}{BAI_{-10}}$$

In order to examine factors influencing radial growth response I used an analysis of

covariance run in RStudio 3.3.2 (R Core Team). Specifically, GR was linearly related to the

independent variables site, treatment, age of tree at time of treatment, basal diameter at the time of

treatment, elevation, tree vigor, and total basal area of the plot at the time of sampling. Included in

the model were the interactions of site with tree age, elevation, tree vigor, plot basal area at time of

sampling, tree basal diameter at time of treatment, and treatment. The importance of these factors

and interactions were assessed at a significance level of 0.05.

Two-sample t-tests were conducted to evaluate differences between the average GRs of trees

in the control areas and the trees in the treated areas. The data were checked for possible outliers

using both Tukey's Range test and an analysis of the standard deviations around the mean

(Grayson 2017 *in progress*, Tukey 1977). Tukey's Range test defines potential outliers as points

that are greater than the value of the third quartile + 2.2 times the inter-quartile range or IQR, and

values less than the first quartile – 2.2IQR (Tukey, 1977, Hoaglin et al. 1986). Commonly, the

multiplier used for this test is 1.5 time the IQR, however, further analysis by Tukey and others

favored the multiplier 2.2 (Hoaglin and Iglewicz, 1987). The analysis of the standard deviations

looked for points that were more than two standard deviations away from the mean and identified them as possible outliers. The other conditions necessary to perform a two-sample t-test were also checked. Independence of the trees within plots was assumed, in part because none of the trees were taken from clusters. Normality of the data was evaluated visually using histograms and normal-quantile plots.

Finally, a subsample of the trees was used to analyze the height growth of treatment and control trees. Since all five discs needed to be processed and aged to allow comparison of height growth over the lives of the trees, only the trees sampled during the 2016 field season were used. In order to analyze the height response of the tree over the period, I plotted the numbers of growth rings on a given disc against the corresponding disc height to create a growth profile. In total, six measurement points were available. The base disc (measurement point #1) had a height of zero and an age corresponding to the total age of the tree. The tip measurement point (#6) corresponded with the total height of the tree and had a matching age of zero since it represented the lowest height not yet surpassed by the tree.

Results

All of the long-term monitoring plots, treatment and control, showed a decrease in stand basal area between the pre-treatment and post-treatment measurements (Table 5). In the treated units, this decrease is attributed to the treatment that was implemented. In the control units, the agent of mortality was unable to be determined, however all tree species were affected equally. The time between measurements at the monitoring plots did not allow us to determine exactly when the mortality occurred. Pre-treatment basal areas in the treatment unit monitoring plots ranged from 21.44 m² ha^{-1}, at Coyote Meadows, to 59.73 m² ha^{-1}, at Bear Overlook. In the control

units, the basal areas of the monitoring plots before treatment ranged from 32.52 m² ha^{-1}, at Bear Overlook to 63.16 m² ha^{-1} at Snow Bowl (Table 6, Figure 4). After the treatments, the basal areas of the monitoring plots in treated units ranged from 0.15 m² ha^{-1}, at Beaver Ridge, to 37.04 m² ha^{-1} at Snow Bowl. The basal areas of the control units post-treatment ranged from 11.08 m² ha^{-1} at Coyote Meadows to 36.04 m² ha^{-1} at Snow Bowl (Table 6).

In total I sampled 93 trees, less than 23 cm at DBH, from four sites in Idaho and Montana that received release treatments between 1999 and 2001. Trees sampled from treated units ranged in age from 17 years old to 201 years old, with an average age of 65 years. Trees sampled from the control units ranged in age from 24 years old to 269 years old with an average age of 81 years. Coyote Meadows had the youngest sampled trees with a mean age of 56 years old, while the trees at Snow Bowl were on average the oldest with a mean age of 108 years old (Table 7). The species composition of the four sites was dominated by subalpine fir and whitebark pine in the control plots, and whitebark pine, subalpine fir, and lodgepole pine in the treated units (Figure 5). Saplings had the highest density at greater than 180 trees/ha for all sites.

After aging the samples, I found a weak positive correlation (R=0.55) between tree basal diameters (BD) and ages (Figure 6). The median BD of trees sampled at Snow Bowl was 11 cm and the mean age was 108 years. Beaver Ridge had the smallest median BD of all of the sites at 4.3 cm and a mean sample tree age of 61 years (Table 7). The sample tree site distribution was heavily skewed towards the smaller trees (Table 7).

The average annual basal area increments (mm² yr^{-1}, BAI) for the trees in the four sites varied by treatment (Table 5). At Bear Overlook, the average BAI, before treatment, in the control was 232.43 mm² yr^{-1}, and the average BAI of the thinned and burned unit was 204.05 mm² yr^{-1}. After the treatment, the average BAI of the control unit decreased to 209.98 mm² yr^{-1}, and the average

BAI of the thinned and burned unit increased to 277.07 mm² yr^{-1} (Figure 7). At Beaver Ridge the pattern was the same: average BAI decreased in control units and increased in the treated units (Figure 7). The average BAI increased in all units at Coyote Meadows, though the increases were proportionally greater in the treated units. Conversely, average BAI declined in all unit at Snow Bowl, though the decline was proportionally greater in the control unit (Figure 7). I saw an immediate response to the treatment from the trees in the Bear Overlook, Beaver Ridge, and the burn unit trees in Coyote Meadows. The cut-burn unit at Coyote Meadows and the thin unit at Snow Bowl showed a slight lag before the trees responded to the treatment (Figure 7).

Growth ratios varied greatly among trees and could only be partially accounted for by differences in measured tree, plot, and site factors, with an overall model goodness of $R^2 = 0.53$. Some of the variability in GR was attributable to treatment: in particular, linear modeling results showed that sample trees in treatment units had higher growth ratios than those in control units ($p = 0.0009$; Table 8). In the control units, GR ranged from 0.99 (se = 0.16) to 1.59 (se = 0.22) and in the treated units it ranged from 1.04 (se = 0.15) to 2.67(se = 0.49). Snow Bowl, where the only treatment applied was thinning, showed the smallest difference between the average percent annual growth rates of the treated and control units. The trees in the treated unit at Coyote Meadows, which was thinned and later burned, showed the greatest change in GR when compared to the trees in the adjacent control unit. The treated trees there reported a mean GR of 2.67 (se = 0.49) while the control trees only had a mean GR of 1.44 (se = 0.14) (Table 5).

In addition to treatment effects, modeling results also identified tree age as having an impact on GR, albeit in a manner that varied by site (Table 8, Figure 8). In contrast, the aggregate basal area of the sample tree plots as measured in 2016/2017 did not appear to affect GR (p=0.76; Table 8). This may be because the plots were too large to capture neighborhood tree competition,

or because aggregate basal areas were affected by multiple factors between 2000 and 2016/2017. Similarly, plot elevation did not appear to influence GR, possibly due to the small differences in elevation between plots within sites. Vigor of the sample trees – as measured in 2016/2017 – also did not contribute to the growth ratio changes of the trees in this study. The vigor classifications used in this study were modified from a crown ratio classification system used for ponderosa pine (*Pinus ponderosa* Lawson and C. Lawson) and may not have been sufficient for accurately classifying whitebark pine. Alternatively, the vigor observed in 2016/2017 may not represent the status and dynamics of tree vigor prior to and within 10 years of treatment.

Treatment effects on radial growth

In total, I examined the annual percent growth response of trees in three types of treated areas: thinned units, prescribe burn units, and thinned units that were later burned. Within a site, the mean GR was greater for all of the treated units than the control units (Figure 10). Site-level t-tests indicated that units which were thinned and later burned (Coyote Meadows and Bear Overlook) had a significantly higher GR than controls (p =0.05; Table 5). The difference in mean GR in the burn-only unit at Coyote Meadows was marginally significant (p =0.1). The other burn-only unit, at Beaver Ridge, showed an increase in GR of 2.49 versus 1.59 in the control unit. Yet owing to the small sample size and the high variability of growth rates between trees, the difference between the treated and control means was not statistically significant. The thinned unit at Snow Bowl showed almost no difference in GR between the treated unit and the control unit (Table 5).

Two trees were identified as potential outliers, one at Bear Overlook and one at Beaver Ridge. These trees were growing much faster than the others. They were not removed from the

dataset however, because no errors could be found in the tree data that would have falsely contributed to the reported GR.

Height growth responses

I examined the vertical growth response on a subsample of 28 trees taken from the four sites during the 2016 year of field work. The resulting line graphs showed how quickly the trees increased their statures between sample sections (Figure 11). Trees from both treatment and control units were examined. As with radial growth, graphical examination of the trees' vertical response showed a wide degree of variability between trees. In general, all of the trees showed similar growth patterns between the first (base disc) and second discs. At this point, the majority of the trees were old enough that the growth they exhibited between these cuts was manifest before any treatment took place. However, data from the 3rd, 4th, and 5th discs suggest that the trees in the treated areas increased height at a faster rate than the trees in the control areas (Figure 11). Beaver Ridge and Bear Overlook showed the least amount of difference in height growth between treated and control trees. These two sites also showed the most variability between trees in the same treatment or control units. The treatment trees at Coyote Meadows and Snow Bowl clearly increased in height faster than the control trees. The increase was most dramatic at Coyote Meadows between the 3rd and 4th cuts while the increase at Snow Bowl was more gradual and less variable (Figure 11), though only four trees were measured at that site.

Discussion

Given the rapid decline of whitebark pine throughout much of its range, and the expense of habitat restoration, the question of whether and how whitebark pine regeneration respond to treatments is one crucial for future management of the species. This study is the first to examine

the radial and vertical response of whitebark regeneration to release treatments. I sampled trees in treatment and control plots, located within four long-term monitoring sites treated circa 2000. Overall, I found that trees in treated areas showed a greater relative increase in radial and in vertical growth than trees in control units. However, the variability in growth was also greater among trees in treated units and could not be attributed to any single treatment factor.

Related studies

A previous study found similar results in mature whitebark pine. Keane et al. (2007) examined stem cross-sections from 59 mature whitebark pine sampled from 21 logged stands where most of the competing tree species were removed by the logging activity. Of all the trees sampled by Keane et al., 14 were excluded from the analysis because they did not contain enough rings pre-treatment to calculate baseline growth. Of the remaining trees, more than 80% showed an increase in radial growth. The trees also showed a large amount of variability in their growth response to the treatment. Site specific factors such as temperature and precipitation were also ruled out as the cause for the increased ring width because the year-over-year growth trends did not correlate with these climate variables (Keane et al. 2007). Some trees immediately increased their radial growth, while others experienced a lag of up to 15 years before they showed any response to the treatment. The few saplings in the study decreased in ring growth immediately after treatment. This was attributed to a lack of established root systems and foliage to support the sudden increase in available resources.

My findings are consistent with those of Keane et al. (2007) in regards to increased radial growth in treated stands post-harvest. Since I focused on whitebark pine regeneration, I had a larger sample size with which validate the positive response of smaller diameter trees. Keane et al. had only two saplings in the study that were old enough to have sufficient number of rings

pre-treatment. These two trees showed a decrease in ring width after treatment. My study found that younger trees tended to show a greater increase in GR than did older ones (Table 8, Figure 8). This suggests that once whitebark trees in the understory reach an advanced age they may respond slowly or poorly to release treatments.

Occurrence of mortality in control units

An unexpected issue that I encountered was the amount of amount of tree mortality occurring in the control units post-treatment (Figure 4). In the treated units, the reduction in stand basal area of the monitoring plots occurred mostly around the time of treatment. However, in the control units considerable mortality occurred over time. Since this mortality in the control units occurred gradually, the trees in my sample plots located in those control units are also likely experiencing a gradually diminishing competition regime. As a result, they may be experiencing a slow release. While this could make it harder to detect the direct treatment impact on GR. Although perhaps it is still the appropriate comparison because treated areas ought to be compared against conditions that would arise in the absence of treatment.

Lag time before release

In my study I focused specifically on the average growth 10 years pre- and post-treatment for each tree. Due to this short time window I were unable to fully examine the duration of the release that the trees experienced (Figure 7). I were also unable to examine the presence or effects of lag time, or the full duration of any lag time (Figure 7). Some of the trees in the study by Keane et al. (2007) still showed positive ring width responses up to 20 years after the harvest. Additionally, other trees experience lag times of up to 15 years before responding to the release treatment. The narrow window of time my study examines does not allow us to determine how long the whitebark regenerations response to treatment lasts. It also constrains my ability to

determine if trees that do not show a significant increase in GR are simply experiencing a lag due to the sudden removal of competition after treatment and will eventually respond or will simply never respond.

Sources of Variability

The universally high degree of variability among trees was only partially attributed to measured site and tree factors ($R^2=0.32$). The unexplained portion could be due to a variety of factors such as variations in microsite, competition, or exposure. Most notably, the variability between trees in the control area was less than that of the treated areas except at Snow Bowl (Table 5). In the control sites, the basal area of the plots were fairly similar plot to plot, there was also less variability in the GR of the trees. In the treatment units, the basal area of the plots varied greatly and there was more variability in the GR of the sample trees (Table 6). Because I did not measure neighborhood competition from other trees within the plot and near the sample trees, my models were unable to determine if this affected GR. However, treatment had significant effects on GR and treatment was linked with plot basal area, at least at the time of treatment. The treatment was designed to affect plot basal area and the impacts on GR are broadly attributed to the removal of plot basal area (Figure 9).

Limiting factors such as nutrients, water, or light, can change how the tree responds to changes in the environment (Poorter and Nagel 2000). It may be that some of the younger, smaller sample trees were limited by nutrients or foliage and existing root systems and therefore showed more variability in their annual growth when compared to other small trees from the same site. Additionally, older, larger trees have more developed crowns and, presumably, root systems, and may be less reactive to site-specific seasonal variation thereby reducing the amount of variation in GR (Poorter and Nagel 2000).

Furthermore, some of the variability observed in GR may be due to tree genetics. Liu et al. (2016) found clear genetic differentiation among seed families and spatial patterns of several genetic subgroups of whitebark pine. Genetic analyses were not part of this study, however the study sites are spatially dispersed (Figure 1) so it is reasonable to assume that there is some genetic variation between the seed sources at the four sites and that that may be contributing to some of the observed variation. In addition to genetic variation, some of the variability between individual trees may be traced back to the seed source. Leirfallom et al. (2015) examined seedling density and seed source health (health defined as parents that were rust and beetle free). Their study found a higher density of seedlings in areas with healthy seed sources suggesting that healthy parents lead to healthy offspring. Trees from healthy seed sources may grow and respond better to release treatments than trees from unhealthy seed sources.

Implications of Increased Growth

Most researchers agree that without help from restoration efforts whitebark pine will be lost from much of its native range (Tomback et al. 2016). Restoration methods commonly focus on increasing the rate of growth of whitebark pine to decrease the time it takes to reach maturity. By reaching cone-producing maturity sooner, these trees will continue to maintain the genetic diversity of the population (Robinson and Wareing 1969, Tomback et al. 2016). Yet research suggests that there are benefits and downsides to this goal.

Smaller trees face more challenges to survival and growth than large, established ones. They are often preyed upon by herbivores and must compete for light and other resources with other trees and vegetation. Price (1991) examined the response of young trees and plants to herbivores. He found that as trees and plants grew taller and older the rates of herbivory decreased. He also noted that individual plants and trees exposed to herbivory also tended to

develop chemical or physical defenses during the span of the study. By decreasing the time it takes for a tree to grow out of the reach of most ungulates, managers are shortening the amount of time that it is susceptible to that type of herbivory.

There may be negative effects of improved growth that have not yet been realized due to the lack of long-term research on whitebark response to treatment. Eis et al. (1968) found that commercially grown Douglas fir (*Pseudotsuga menziesii* Franco), grand fir (*Abies grandis* Douglas) and western white pine (*Pinus monticola* Douglas) all showed depressed ring growth during years of heavy cone production suggesting that there is a trade-off between growth and cone production. Climent et al. (2008) found that in Aleppo pines there was a trade-off between growth and cone production. Trees which grew vigorously did not allocate as many resources towards cone production and had smaller cone crops than the slower growing trees in the study. Poor cone crops already occur due to white pine blister rust infections and mountain pine beetle attacks. A future generation of trees producing fewer cones could have wide-ranging negative effects on high-elevation ecosystems. Already it has been noted that during years of poor cone production, Clark's nutcrackers turn into seed predators (Schaming 2015). Mueller at al. (2005) found that herbivory resistant traits in pinyon pines affected seed production. Trees with more resistance produced larger cones with more seeds. By increasing growth rates, managers may be inadvertently encouraging the trees to by-pass building resistances that they may need for the future. However, no research has been done on whitebark pine to show cone crops or tree resistance is affected negatively by increased growth rates.

Lastly, much research has focused on the tree size preference of mountain pine beetles. Increasing the growth of whitebark pine regeneration may make them more susceptible to beetle attacks before they have sufficient defenses (Raffa et al. 2013). With warming climates,

whitebark pine are being exposed to more beetle attacks and the beetles are targeting smaller trees. Bentz et al. (2015) found that even though mountain pine beetles were more likely to attack lodgepole pine, when they did attack whitebark pine, the beetles were more likely to mount a successful attack. Dooley et al. (2015) collected results showing that mountain pine beetles were attacking smaller diameter whitebark pine than lodgepole pine in the same area, and also showed that the emergence rate of beetles from a successfully attacked whitebark pine were higher when compared to similarly attacked lodgepole pine. Such results highlight the need for thorough research on the implications and outcomes of restoration activities.

Restoration and Management implications

Despite the difficulties of restoring high-elevation ecosystems, managers are beginning to implement treatments which aim to mimic the structure of historic whitebark pine stands. Whitebark pine has a competitive advantage until more shade-tolerant species begin to take over (Keane and Parsons 2010). With the continued suppression of wildfire in whitebark pine environments, managers are relying on silvicultural cuttings as a means of restoring whitebark pine to the landscape. These treatments are usually used in stands with large proportions of suppressed whitebark pine in the understory. By reducing competition, suppressed trees have access to more resources and therefore a greater probability of surviving, showing increased growth rates and eventually developing into cone-producing adults (Keane et al. 2007).

The study sites for this project are part of an on-going monitoring project, established in the mid-1990's, which applies a mix of silvicultural treatments and prescribed burns to five whitebark sites in the Bitterroot Range to examine the outcome of restoring whitebark pine ecosystems to historic stand structures. Ten-year results from Keane and Parsons (2010) show that whitebark presence is increasing in these treated areas. There is also a low prevalance of blister rust in new

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seedlings and little to no signs of mountain pine beetle attack in mature trees (Keane and Parsons 2010). The main drawback of restoration efforts like these are that they are very labor intensive, practical only on a small-scale basis, and limited by road access. Prescribed burns can only be conducted during a small window of time, are expensive to carry out, and labor intensive. They provide a short-term solution for managers seeking to save current populations of whitebark pine. Results from growth analysis projects like ours, which examine how how advanced-aged whitebark regeneration respond to treatments, add additional evidence that whitebark respond to a variety of restoration methods. However, due to the difficulties of restoring large areas of whitebark habitat, it is unlikely that these techniques will be effective for range-wide restoration.

Another restoration strategy hinges on collecting cones from whitebark pine trees that show blister rust resistance, germinating the seeds in a greenhouse setting and then planting the seedlings back into old burns (Mahalovich et al. 2006). Combining restoration and modeling work may be key for the success of future projects as it maximizes the efficiency of on-the-ground efforts and restoration funds. Ultimately the success of whitebark management and restoration will hinge on collaborative efforts across its whole range, even while the effectiveness of these effort may not be known for decades.

Conclusions

Whitebark pine is widespread in the high-elevation ecosystems of western North America. Its loss could have cascading impacts on many other species and lead to landscape-level changes. The results from this study show that whitebark pine regeneration can respond to release treatments. Younger trees showed higher GR than older trees, and most trees in thin-burn and burn only units had higher GRs than trees in thin-only or control units. Not all treatments were implemented on all sites and trees at some sites responded better to treatments. This highlights the need for designing

future studies where treatments are closely replicated across sites. Already there is a large amount of variability in GRs owing to site and stand factors – heterogeneity in treatment intensities and outcomes further complicates analyses. If the primary mechanism by which release treatments impact regeneration is through basal area reduction then more controlled conditions would be necessary to identify those effects. Future monitoring studies and restoration efforts should be closely paired to better understand where treatments would be most effective given the variability of high elevation ecosystems.

There is much debate about how whitebark pine will respond to modified wildfire regimes, mountain pine beetle outbreaks, and blister rust attacks as climates change. It is, however, widely agreed upon that restoration will be key to this species' survival. Climate change will likely become more of a challenge for managers as they make decisions about allocating resources and limited funding. Collaboration between researchers, modelers, and managers will be essential to ensure the best decisions are made using recent, relevant research that will maximize the direct benefits to whitebark pine. Current restoration efforts should be continued, as they will be vital to the long-term survival of whitebark pine.

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Tables

Table 1: Description of study sites.

Study Site	National Forest	Elevation (m)	Aspect	Habitat Type	Cover Type	Year of Treatment
Bear Overlook	Bitterroot, MT	2088-2149	Southeast	ABLA/LUHI ABLA/MEFE	PICO/ABLA	1999
Beaver Ridge	Clearwater, ID	2134-2179	South	PICO/LUHI	PICO/ABLA	1999
Coyote Meadows	Bitterroot, MT	2377-2438	Southwest	PIAL/VASC	PIAL/ABLA	2000
Snow Bowl	Lolo, MT	2164-2195	Southwest	PIAL/LUHI	PIAL/ABLA	2001

Habitat type is taken from Pfister et al. (1977). ABLA is *Abies lasiocarpa* Hook, LUHI is *Luzula hitchcockii* Hamet-Ahti, VASC is *Vaccinium scoparium* Leib, and MEFE is *Menziesia ferruginea* Smith.

Cover type acronyms are PIAL-*Pinus albicaulis* Engelm, ABLA– *Abies lasiocarpa* Hook, *PICO– Pinus contorta* Loudon.

Table 2: Characteristics used to select and rate sample trees adapted from Keen (1943) and

modified using Kipfer (1992).

Full vigor	**Crown**- Full vigorous crowns, with a live crown ratio of 55% or more, average width or wider with density average or better **Foliage**-Needles are average length or longer, dense clusters **Position**- usually isolated or dominant, rarely codominant with regard to the other trees close by
Good to fair vigor	**Crown**- Good to moderately vigorous crowns, with a live crown ratio of 30-55% assuming average width and density; or a longer crown if narrow or somewhat thin, not sparse or patchy **Foliage**- Needles average length, dense clusters **Position**- Usually codominant, but sometimes isolated or dominant, rarely intermediate
Fair to poor vigor	**Crown**- Fair to poor crowns, with live crown ratios of 10-30% if of average width and density, or long, sparse, narrow, or flat on one or more sides **Foliage**- Needles are often short and thinly distributed, but of normal length and density when confined to top 1/3rd of crown **Position**- Usually intermediate, sometimes codominant or suppressed, rarely isolated
Very poor vigor	**Crown**- Live crown ratio less than 10%, sometimes only a tuft at the top of the tree, or somewhat longer when sparse and ragged, usually very narrow or limbs all on one side **Foliage**- Needles often short, and foliage sparse or scattered, or only tufts at ends of branch; but of normal length and density if reduced in quantity **Position**- Usually suppressed or intermediate, but may occur in other positions if greatly reduced in vigor

Table 3: Definitions of terms used to describe sample trees

Symmetrical:	tree looks the same from all sides- tree is conical
Asymmetrical	tree's foliage is clustered to one side, tree has holes in the branch pattern, lopsided
Wispy	tree branches look weak, droopy, tree is abnormally tall given its DBH (example: class one tree, 15 ft. tall)
Stocky	tree has very sturdy branches, tree is short and stout
Needles clustered	needles spread along less than half of the branch
Needles spread	needles spread along half or more of the branch
Many branches	five or more per whorl
Few branches	three or less per whorl
Branches thick	individual branch diameter is more than a quarter that of the tree diameter
Branches thin	individual branch diameter is less than a quarter that of the tree diameter

Table 4: Distribution of sample trees by vigor classification and basal diameter.

	Class 4	Class 3	Class 2	Class 1
0-2.54 cm	8	9	9	7
2.55-10.16 cm	8	8	8	7
10.3-22.86 cm	10	7	6	3

Table 5: Sample sizes, average change in annual growth rate, standard errors, and pre- and post-treatment basal areas (m^2ha^{-1}) by treatment unit and site.

Site	Treatment	n	pre-BAI	post-BAI	μ GR	se GR
Bear Overlook	Control	10	232.43	209.98	1.09	0.17
	Thin. Burn	10	204.05	277.07	2.34**	0.51
Beaver Ridge	Control	12	984.78	939.86	1.59	0.22
	Burn	8	335.28	627.25	2.49	0.62
Coyote Meadows	Control	12	574.32	648.53	1.44	0.14
	Burn	8	123.38	225.84	2.67*	0.49
	Thin. Burn	11	903.58	1232.97	2.25**	0.29
Snow Bowl	Control	13	676.78	519.90	0.99	0.16
	Thin	9	545.64	520.22	1.04	0.15

n= number of trees

se GR= standard error of mean growth ratio= standard deviation/√n

** = statistically significant difference at p= 0.05

*= statistically significant difference at p= 0.1

BAI pre= average growth before treatment (mm²/yr)

BAI post= average growth after treatment (mm²/yr)

μ GR- mean growth rate (postBAI/preBAI)

Table 6: Pre- and post- treatment basal areas (BA; m^2 ha^{-1}) in the long-term monitoring plots

Site	Treatment	Pre-BA	Post-BA
Bear Overlook	Control	32.52 (1996)	19.96 (2015)
	Thin. Burn	45.12 (1996)	21.01 (2000)
Beaver Ridge	Control	36.36 (1997)	18.98 (2005)
	Burn	25.90 (1997)	0.15 (2005)
Coyote Meadows	Control	37.59 (1993)	11.8 (2003)
	Burn	30.56 (1993)	5.25 (2001)
	Thin. Burn	21.44 (1993)	1.76 (2001)
Snow Bowl	Control	63.16 (1996)	36.04 (2004)
	Thin	59.73 (1996)	37.04 (2002)

Pre- BA= average pre-treatment basal area/ha (m²/ha), collected from the monitoring plots before the treatment occurred, the year of data collection is in parentheses after the BA

Post-BA= average post-treatment basal area/ha (m²/ha), collected from the monitoring plots (1-15) years after treatment occurred, the year of data collection is in parentheses after the BA

Table 7: Age and basal diameter (BD) characteristics of the trees in the control and treatment

units at the four sites.

Site	Age Range (yrs.)	Mean Age	Median BD (cm)	Mean control age	Mean trt. age
Bear Overlook	20-201	74.3	5.21	67.6	80.9
Beaver Ridge	24-113	61.3	4.32	58.3	65.6
Coyote Meadows	17-118	56.3	5.33	67.3	48.2
Snow Bowl	40-269	108.4	11.05	125.9	83.0

Age range: youngest to oldest sample trees from the site

Mean age: average age of all tree from the site

Median BD: median used instead of average basal diameter due to the high number of small trees

sampled

Mean control age: average age of the trees sampled in the control units

Mean trt.age: average age of the trees sampled in the treatment units

Table 8 : Analysis of covariance results for the growth ratio model based on all sample trees (df = degrees of freedom; ** = significant at 0.05 level; * = significant at 0.1 level).

Factor	df	*F-value*	P-*value*
Site	3	6.78	0.09*
Treatment	3	6.47	0.0009 **
Tree age at treatment	1	8.86	0.000008**
Elevation	1	0.29	0.59
Tree vigor	1	0.33	0.57
Tree basal diameter at treatment	1	0.13	0.72
Plot basal area (2016/2017)	1	0.09	0.76
Site×Treatment	2	0.13	0.87
Site×Tree age at treatment	3	3.33	0.03**
Site × Elevation	3	1.25	0.29
Site× Tree vigor	3	0.15	0.92
Site× Plot basal area (2016/2017)	3	0.71	0.54
Site× Tree basal diameter at treatment	3	0.59	0.62

Figures

Figure 1: Location of the four sample sites (image generated in Google Earth Pro 2017)
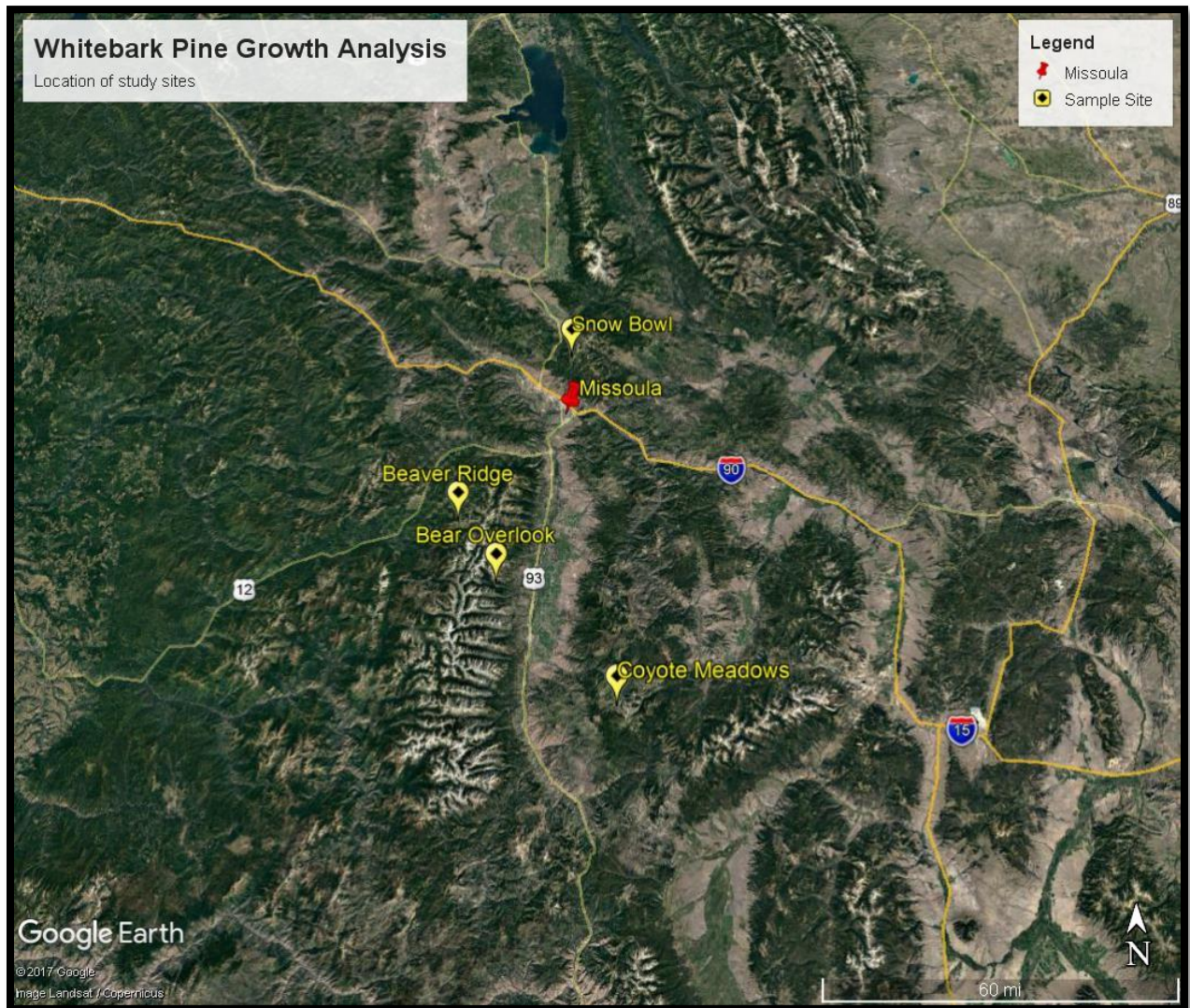
Figure 2: Schematic of plot layout with nested microplot

**2.1 m radius
Seedling plot
(0.001 hectare)**

Plot center

**11.3 m radius
Tree & Sapling plot
(0.004 hectare)**
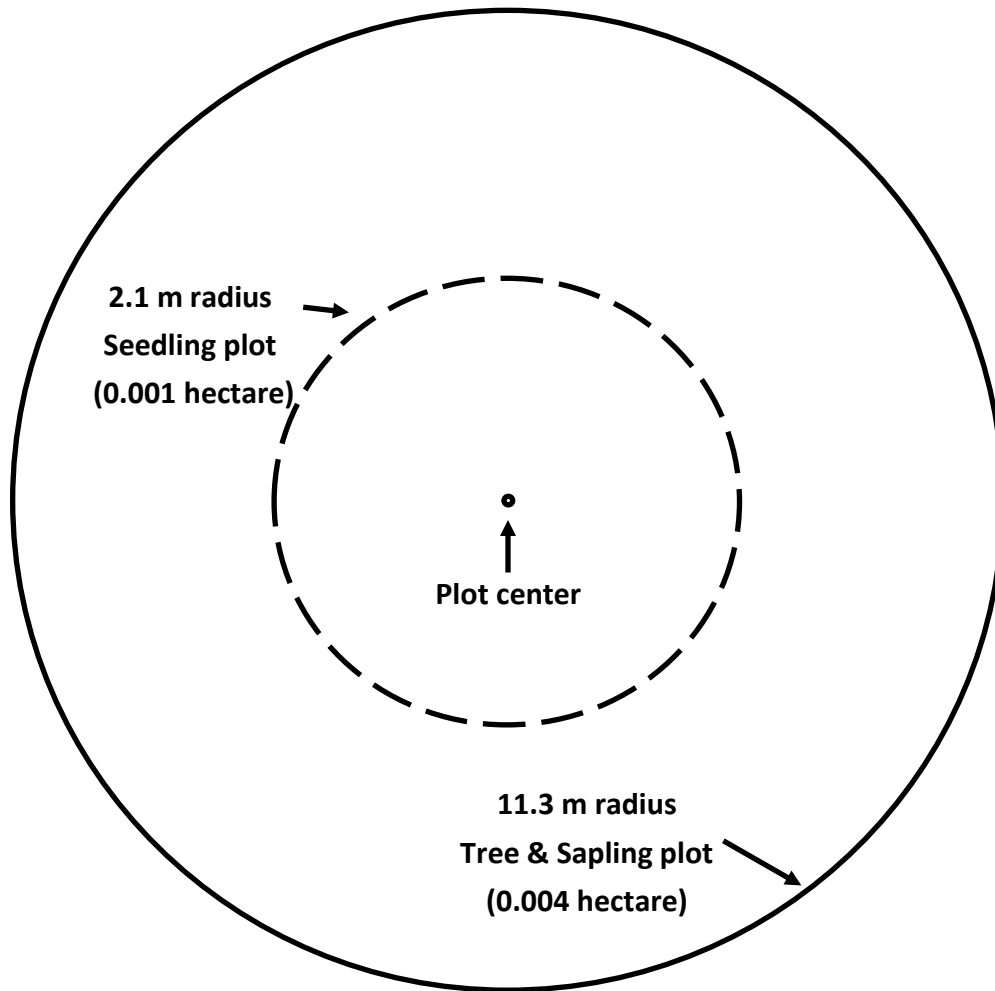
Figure 3: Example of visual differences in the identifiability of tree rings on a disc after scanning

(A) and after the same disc was dyed light purple and prepared as a slide (B).
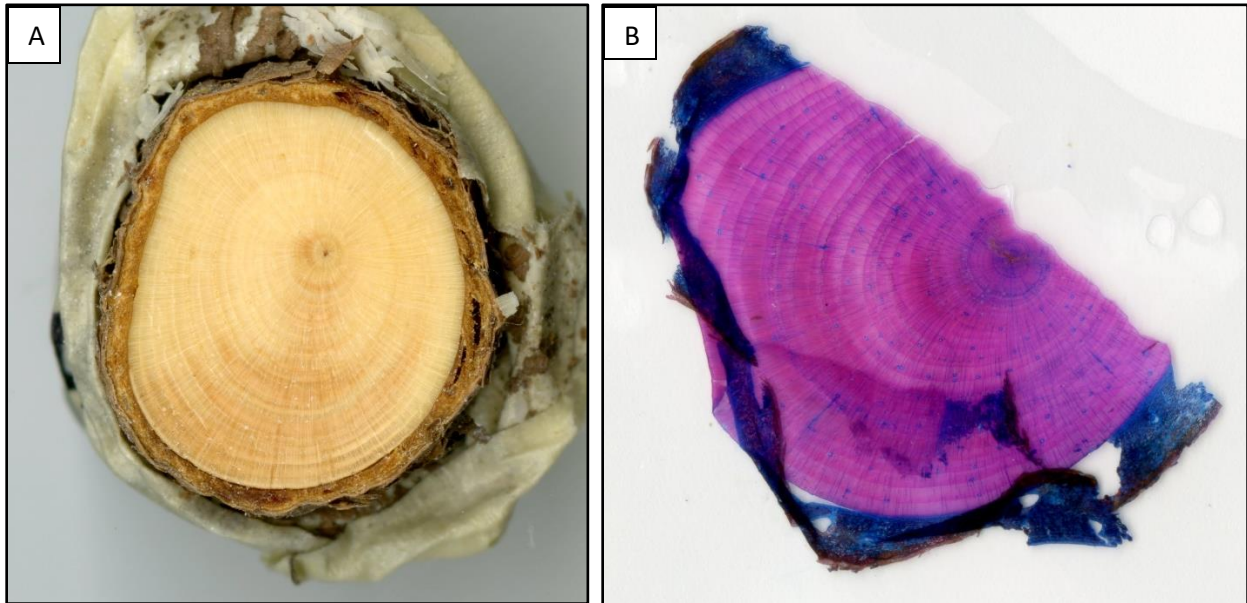
Figure 4: Changes in stand basal area (m^2 ha^{-1}; live trees above 11.3 cm DBH) observed in the long-term monitoring plots across the four study sites (CM: Coyote Meadows; SB: Snowbowl; BO: Bear Overlook; BR: Beaver Ridge). The black line (year 0) indicates when treatment occurred
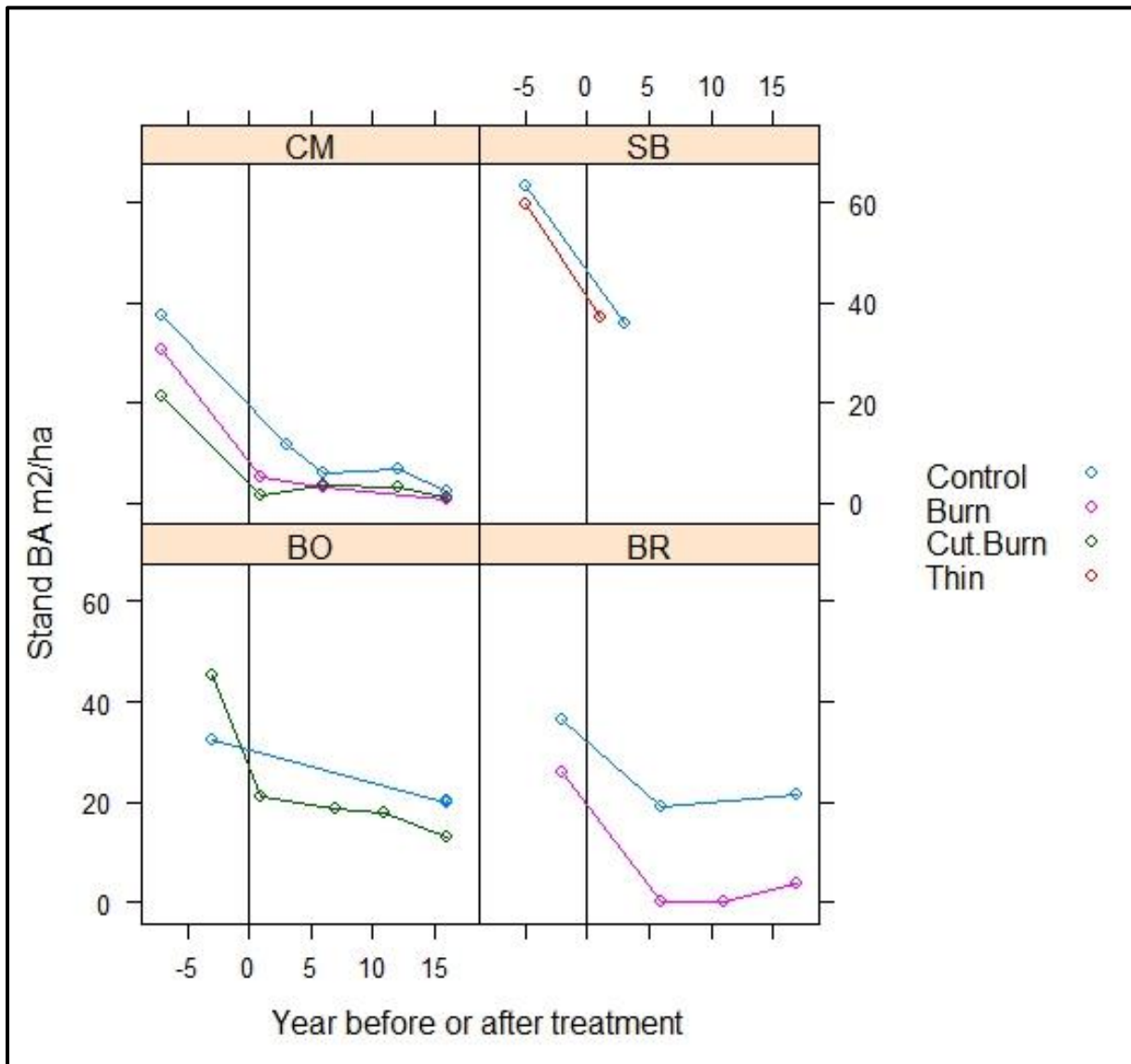
Figure 5: Species composition in 2016 by size class (trees: DBH > 11.4 cm; saplings: $11.4 \geq$ DBH > 0 cm; seedlings: height < 1.37 m), treatment, and site (CM: Coyote Meadows; SB: Snowbowl; BO: Bear Overlook; BR: Beaver Ridge). Tree counts derived from the same plots from which sample trees were drawn.
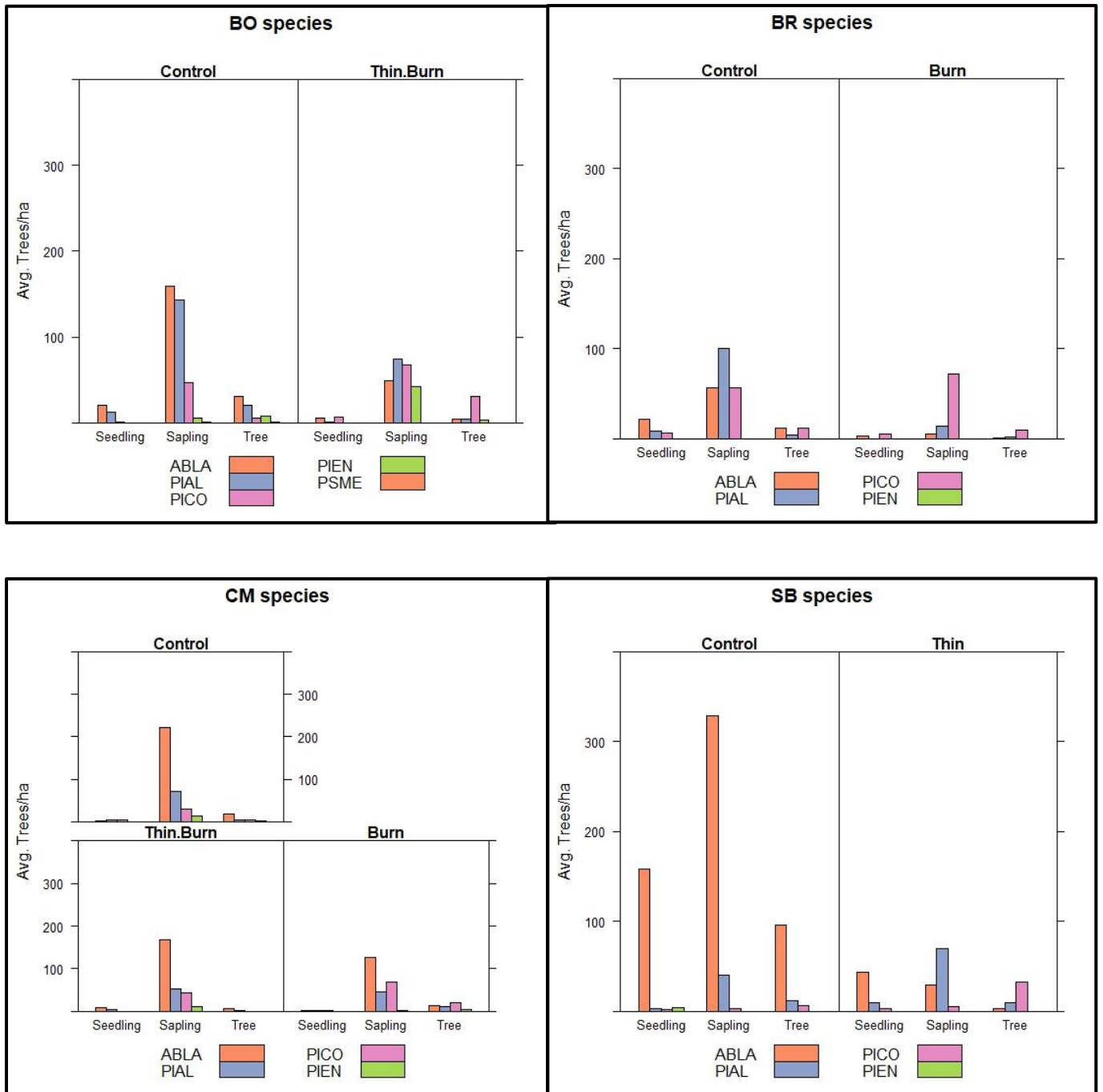
Figure 6: Relationship between sample tree DBH and total age across all sites, R= 0.55
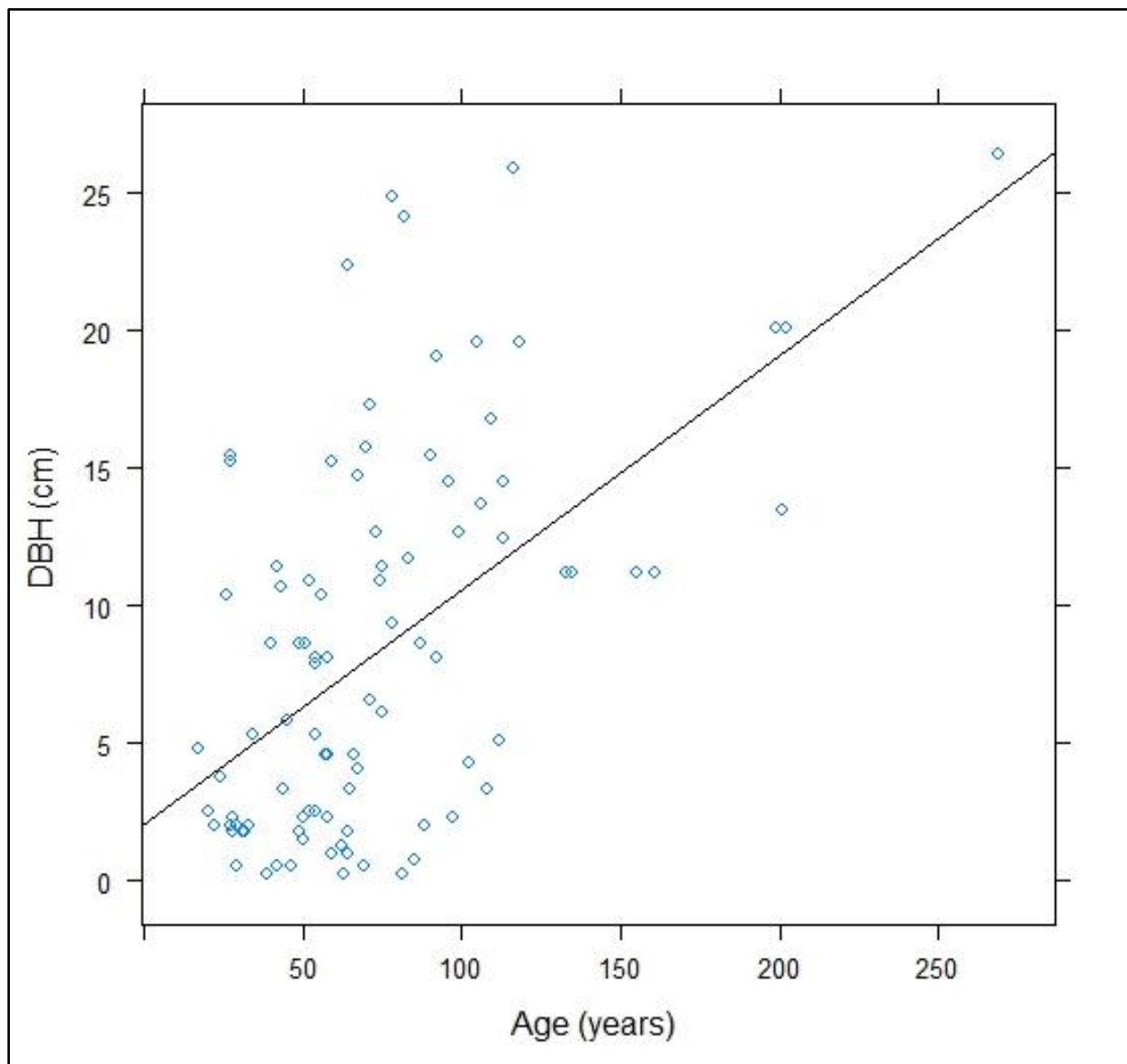
Figure 7: Mean basal area increments (BAI; mm^2 yr^{-1}) over time for sample trees in the control and treated units. The black line indicates the year treatment occurred.
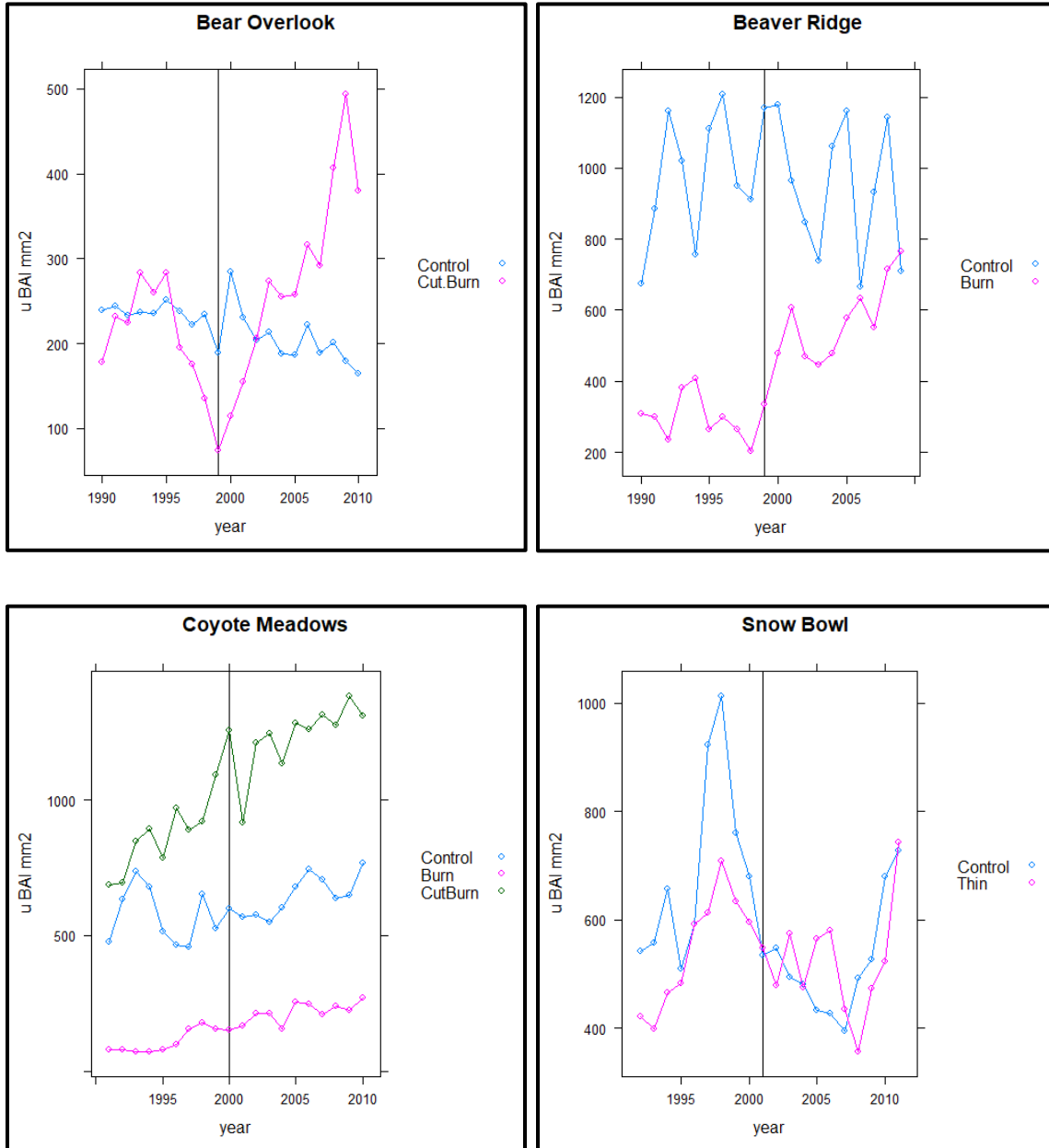
Figure 8: Relationship between growth ratio and tree age by site (CM: Coyote Meadows; SB: Snowbowl; BO: Bear Overlook; BR: Beaver Ridge).
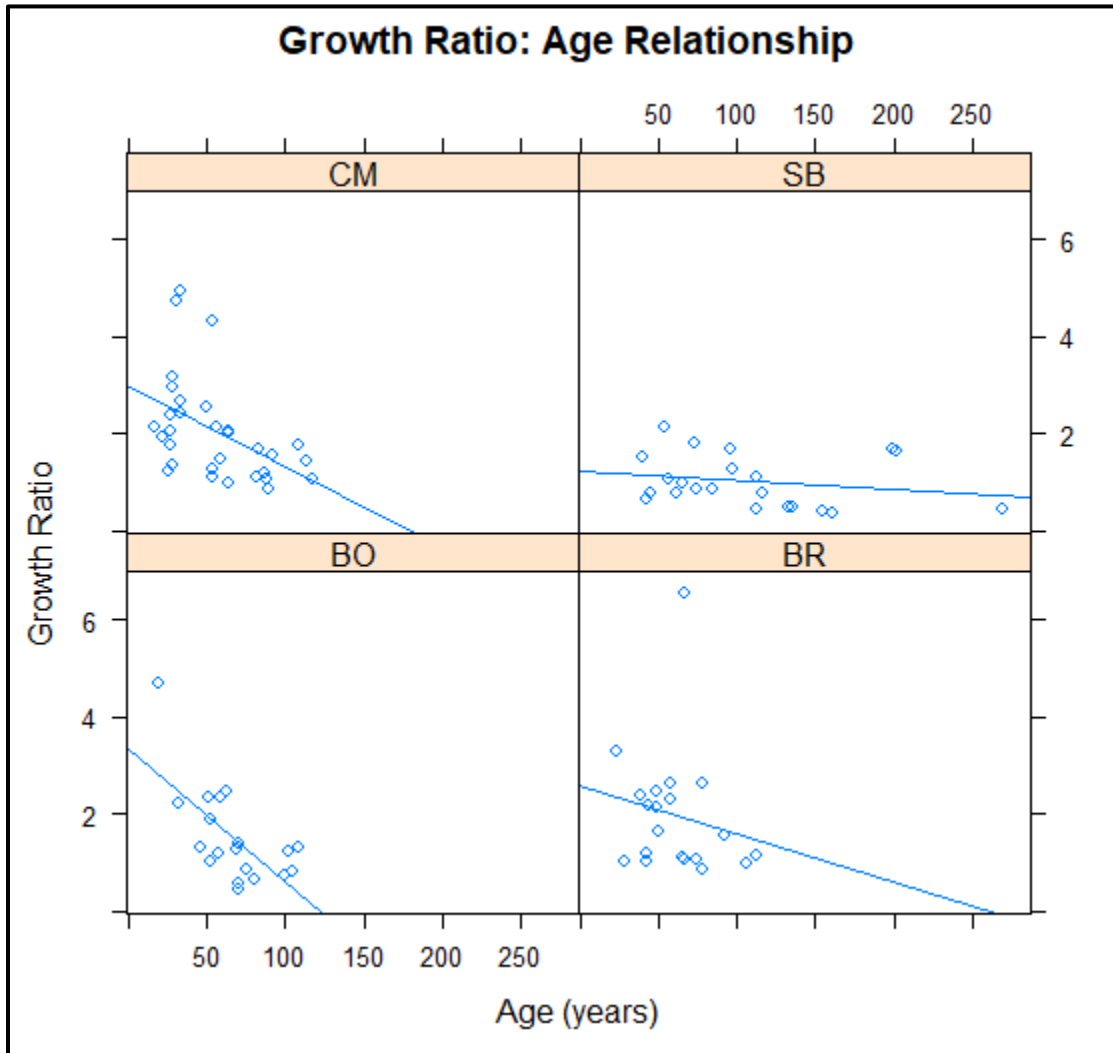
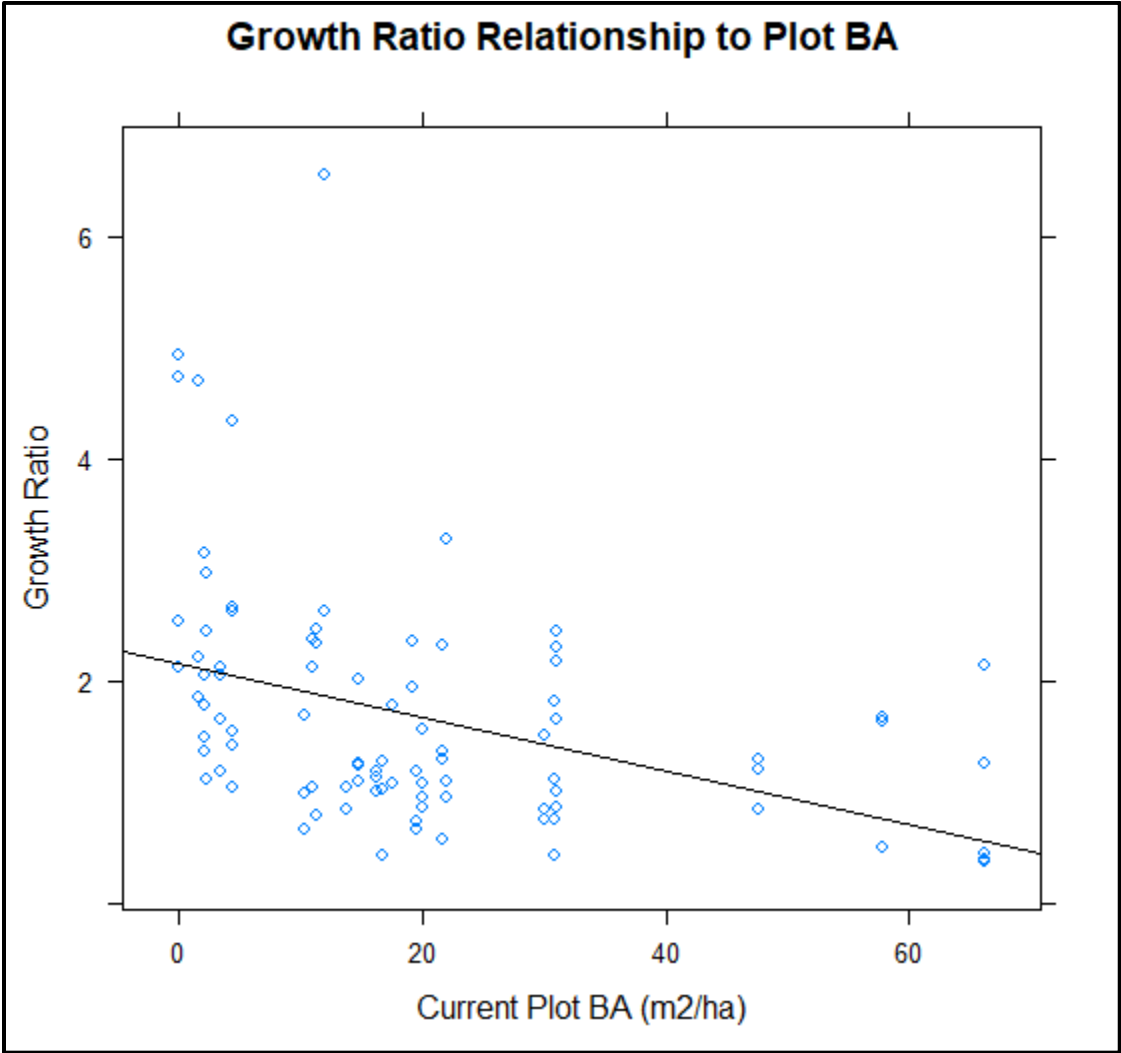Figure 9: Relationship between growth ratio and plot basal area for all sample trees

Figure 10: Distribution of growth ratios in treatment and control units at each site. Significance of differences between treatment and control means indicated by asterisks (** = significant difference at p= 0.05; *= significant difference at p= 0.1)
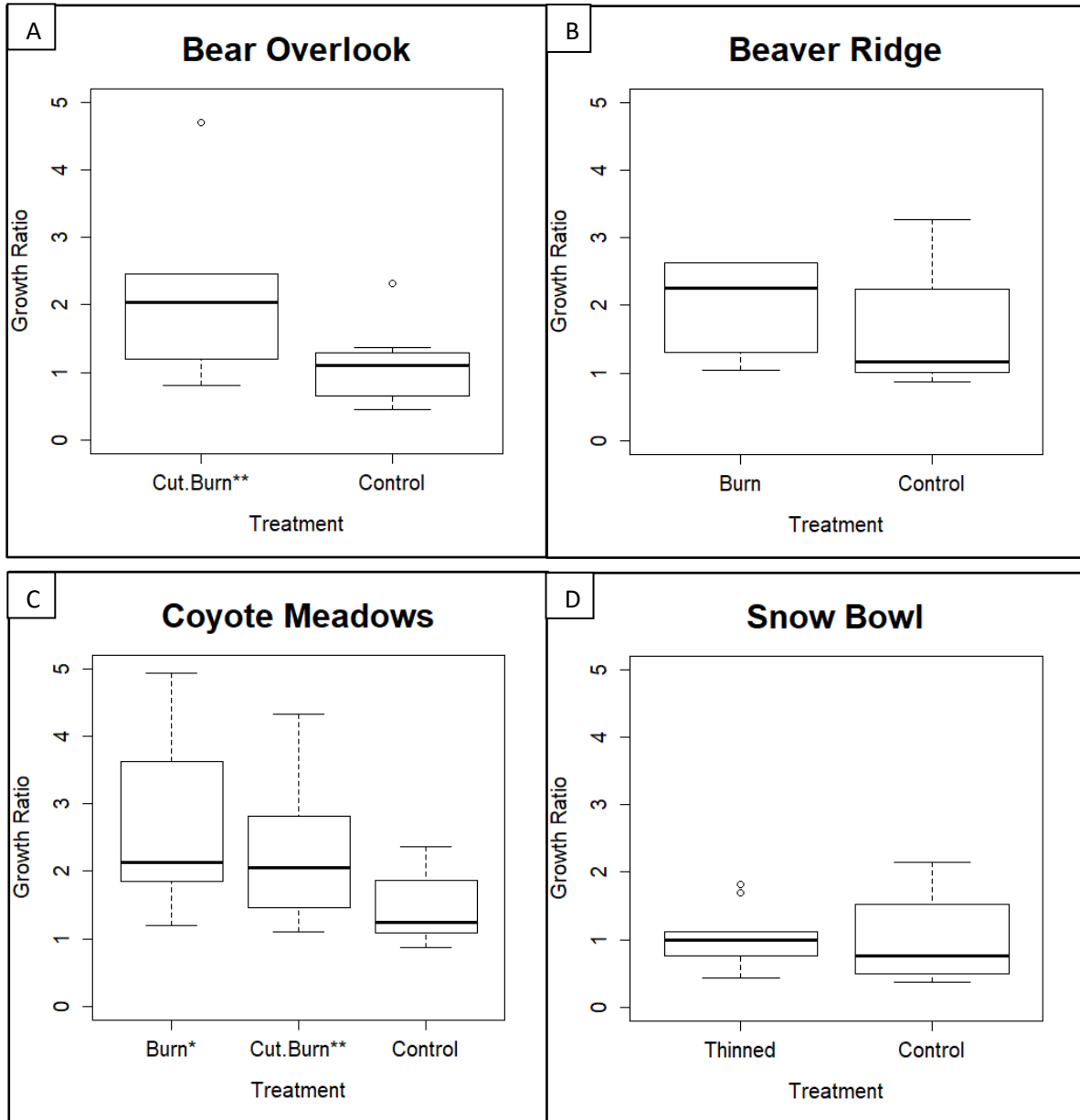
Figure 11: Height profiles of individual sample trees in the treated and control units by site (BO= Bear Overlook, BR= Beaver Ridge, CM= Coyote Meadows, SB= Snow Bowl). The black vertical line indicates the year of treatment.