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Growth Response of Whitebark Pine (*Pinus albicaulis* Engelm) Regeneration to Thinning and Prescribed Burn Treatments

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Abstract: Whitebark pine (*Pinus albicaulis* Engelm.) forests play a prominent role throughout high-elevation ecosystems in the northern Rocky Mountains, however, they are vanishing from the high mountain landscape due to three factors: exotic white pine blister rust (*Cronartium ribicola* Fischer) invasions, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, and successional replacement by more shade-tolerant tree species historically controlled by wildfire. Land managers are attempting to restore whitebark pine communities using prescribed fire and silvicultural cuttings, but they are unsure if these techniques are effective. The objective of this study was to determine how whitebark pine regeneration responds to selective thinning and prescribed burn treatments. We studied changes in diameter growth after restoration treatments using ring width measurements obtained from 93 trees at four sites in Montana and Idaho that were treated in the late 1990s. Overall, the average annual radial growth rates of the trees in treated areas were greater than those of trees in control areas. Specifically, there were significant increases in the growth ratio (180%) in the two sites that were both thinned and later burned. Younger regeneration showed more response to the treatments than older regeneration. All sites showed high variability in post-treatment growth rates across individual trees, with greater variability for trees in treated areas than in trees from the control areas. Results suggest that whitebark pine regeneration can respond to thin and burn release treatments and that managers may see positive results in areas that are treated similarly.

Keywords: whitebark pine; regeneration; release treatments; restoration; radial growth

1. Introduction

Whitebark pine is a foundation species throughout high-elevation forests of the western United States and Canada [1,2] because it promotes biodiversity and stabilizes ecosystem functions such as water quality and quantity regulation [1,3,4]. This slow-growing, long-lived species is well-adapted to the harsh environment where other tree species often struggle [5]. Whitebark pine is an important food source for over 110 animal species [6]. Its large seeds are eaten by many creatures including black bears (*Ursus americanus* Pallas), grizzly bears (*Ursus arctos horribilis* Linnaeus), red squirrels (*Tamiasciurus hudsonicus* Erxleben), and most importantly, Clark's nutcrackers (*Nucifraga columbiana* Wilson) [4,6]. Whitebark pine has a mutualistic relationship with the nutcracker, relying on the bird to disperse its heavy, wingless seeds [4]. The Clark's nutcracker harvests seeds from the whitebark pine cones and carries them as far as 60 km away from the parent tree to plant in caches of 1–15 seeds [7].

Invariably, some of these caches are forgotten and the seeds later germinate to create the whitebark pine forests of tomorrow [4,5].

Whitebark pine ecosystems typically experience three distinct types of fire regimes: low-severity, mixed-severity, and stand-replacing. Low severity fires are non-lethal underburns that reduce fuel loads and top-kill vegetation. They generally do not damage whitebark pine but remove subalpine fir regeneration [8–10]. 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 [8]. Mixed-severity fires generally occur every 60–300 years and usually create burn patches less than 50 hectares in size [9]. These mixed-severity burns include areas of unburned, non-lethal underburns, and stand replacing fire [8]. In areas with sparse surface fuels, fires can burn in a fine-scale patchy mosaic, allowing some mature whitebark pine to survive. Whitebark pine's main competitors, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall), typically have foliage extending much closer to the ground, making them more susceptible to crown scorch, crown fire, and dying from fire. Increased fuel loads or high winds can increase the severity of the fire [8,9] leading to the death of many trees; the majority of whitebark pine stands in the northern portions of the species' range establish after large stand-replacing fires. Whitebark pine is generally the first species to reestablish in large, severely burned high-elevation areas because the Clark's nutcracker disperses its seed up to two orders of magnitude further than wind can disperse seeds of its competitors and has specific physiological traits, such as its ability to tolerate drought [10]. As a pioneer species, whitebark pine often facilitate the establishment of other conifer species, particularly subalpine fir and Engelmann spruce [11,12].

Whitebark pine forests are currently experiencing a severe decline across most of their range in western North American due to the interactions of an invasive fungal pathogen, native bark beetles, and successional replacement by more shade-tolerant species due to fire exclusion. White pine blister rust (*Cronartium ribicola* Fischer) is an exotic pathogen that attacks most five-needle pines, but is particularly deadly to whitebark pine [5,13,14]. This disease was introduced into North America around 1900 on eastern white pine (*Pinus strobus* Martínez) seedlings grown in European nurseries [15]. By the 1950s, white pine blister rust was widespread throughout most of North America [16]. White pine blister rust is currently present throughout most of the range of whitebark pine, reducing cone production and killing trees of all size classes [2,17]. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is an aggressive insect, native to western North America that attacks most pine species [18]. Mountain pine beetles reproduce and the developing larvae feed on secondary phloem. The beetles also introduce blue stain fungi (*Grosmannia clavigera* Jeffr, Davidson), which grows into the sapwood. The joint action of larval feeding and fungal colonization kills the host pine tree, as these two processes interrupt water transport and girdle the tree by cutting off the flow of water and nutrients [19]. Current climate-facilitated severe outbreaks have additionally reduced the numbers of large, cone-bearing, whitebark pine, severely depressing the regeneration potential of the species [17,20,21].

Reduction of wildland fires in whitebark pine ecosystems over the last 100 years of the modern fire exclusion era [22,23] has resulted in successional replacement by more shade-tolerant conifers in many whitebark pine forests. As populations of whitebark pine continue to decline, the nutcrackers may consume most of the whitebark pine seeds that they cache, resulting in severe declines in regeneration [24]. Furthermore, with the exclusion of fire from the landscape, forest openings where Clark's nutcrackers may cache seeds are becoming sparser as they are overgrown with shade-tolerant fir and spruce. These shade-tolerant species out-compete existing whitebark pine seedlings [5]. 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 facilitated, since it is unlikely resistant seedlings will mature and produce cones under such heavy competition [25].

The combination of white pine blister rust, mountain pine beetle, and fire exclusion has contributed to a nearly range-wide decline in whitebark pine populations, making restoration

treatments essential for improving whitebark pine populations across the landscape. The dire situation of whitebark pine was acknowledged by its recent listing as both a candidate species under the United States Endangered Species Act [26] and an endangered species in Canada under the Species at Risk Act [27]. 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 [25,28]. Restoration in whitebark pine ecosystems is challenging and costly. Though a variety of proactive actions are used for restoration, such as planting, monitoring, and collecting seed, for this study, we focused only on those treatments that aim to improve tree vigor with the goal of increasing cone crops in the future [29]. Currently, the most effective methods for enhancing tree vigor are believed to be silvicultural cuttings and prescribed burnings that focus on removing shade-tolerant species [3,25,30]. These release treatments are commonly designed to free young and mature trees from undesirable, usually overtopping, competing shade tolerant trees [31,32]. However, little research has been conducted examining the success of release treatments in restoring whitebark pine populations [3]. In this study, we measured the diameter growth of whitebark pine regeneration in stands that were treated using a combination of silvicultural cuttings and prescribed burning. We evaluated growth release primarily as a relative increase in annual radial growth before and after the release treatments of the combination of selective thinning and prescribed burns conducted on the study sites.

Study Objective

The main objective of this study was to examine the change in radial growth response of smaller, non-cone bearing whitebark pine trees, with a diameter at breast height (DBH measured at 1.37 m above ground line) less than 23 cm, to release treatments, focusing specifically on growth ten years pre-treatment and ten years post-treatment. We examined trees from areas that were thinned, prescribed burned, thinned and burned, or retained as controls in the late 1990s and early 2000s. We 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, we evaluated tree, stand, and site conditions within the treatment areas that may have influenced whitebark pine radial growth response.

2. Materials and Methods

2.1. Study Sites

We selected four sites in the Northern U.S. Rocky Mountains (Bear Overlook, Beaver Ridge, Coyote Meadows located in the Bitterroot mountains, and Snowbowl located at the south end of the Mission mountains) that were part of the Keane and Parsons (2010) [3] long-term monitoring study examining whitebark pine restoration through selective thinning and prescribed burnings. The four sites were treated in 1999–2001 (Table 1). All sites were dominated by encroaching subalpine fir with a noticeable decline of whitebark pine. All sites keyed to the *Abies lasiocarpa* (Hook)/*Luzula hitchcockii* (Hamet-Ahti) habitat type ([33] with most on southern aspects from 2100–2400 m above mean sea level. March temperatures ranged from −7.5 degrees Celsius to 4.2 degrees Celsius. Annual precipitation ranged from 66.84 mm to 147.42 mm per year. Pre-treatment measurements were taken by Keane and Parsons (2010) [3] in the mid-1990s in monitoring plots that were re-measured 1-year post-treatment and then every five years for 15–20 years. Details of the pre- and post-treatment conditions, and the implementation of the treatments, are documented in Keane and Parsons (2010) [3].

Each site was composed of a number of treated and control units. The treated units were thinned, burned, or thinned and burned. The control units were left untouched. The species composition of the four sites was dominated by subalpine fir and whitebark pine (in that order) on the control plots, and by whitebark pine, subalpine fir, and lodgepole pine in the treated units. In the thinned

units, three competitive species were removed: subalpine fir, Engelmann spruce, and mountain hemlock (*Tsuga mertensiana* Bong.). Lodgepole pine (*Pinus contorta* Douglas ex Loudon) was not removed because it was assumed that this species did not negatively impact whitebark survival [34]. In burn-only units, prescribed fires were hand-ignited with drip torches, except for Beaver Ridge units, which were ignited via a truck-mounted flame thrower and a heli-torch [3]. Fires were allowed to burn freely, resulting in a mixed-severity fire with unburned areas intermixed with burned patches. Prescribed burn treatments were conducted to kill 90% of the non-whitebark pine trees and leave 90% of whitebark pine trees alive [3]. 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 [3]. Of the mix of treatments in the four study areas, we focused on four treatment types (including control) for this study because of logistical issues: access, time since treatment, and date of measurement. We selected a thinned only unit at the Snowbowl study site, a thinned and burned unit at both the Bear Overlook and Coyote Meadows sites, and a prescribed burn only unit at both the Coyote Meadows and Beaver Ridge study sites (four treatments altogether, including control; Table 1).

Table 1. Location of study sites, year of treatment (Trt), number of units sampled, treatment type, and pre- and post- treatment (Trt) basal areas (BA; m² ha⁻¹) in the long-term monitoring plots in both control and treatment units (Keane and Parsons 2010) [3]. Pre-BA = average pre-treatment basal area, collected from the monitoring plots before the treatment occurred, the year of data collection is in parentheses. Post-BA = average post-treatment basal area, collected from the monitoring plots 1–15 years after treatment occurred, the year of data collection is in parentheses.

Study Site	National Forest, State	Year of Trt	Units	Treatment Type	Pre-Trt BA (m ² ha ⁻¹)	Post-Trt BA (m ² ha ⁻¹)
Bear Overlook	Bitterroot, MT	1999	2	Thin/Burn	45.65 (1996)	21.01 (2000)
			1	Control	32.91 (1996)	20.38 (2015)
Beaver Ridge	Clearwater, ID	1999	2	Burn only	26.2 (1997)	0.16 (2005)
			2	Control	36.79 (1997)	18.98 (2005)
Coyote Meadows	Bitterroot, MT	2000	2	Burn only	30.56 (1993)	5.25 (2001)
			1	Thin/Burn	21.69 (1993)	1.76 (2001)
Snowbowl	Lolo, MT	2001	2	Control	38.03 (1993)	11.81 (2003)
			1	Thin only	60.43 (1996)	37.04 (2002)
			1	Control	63.90 (1996)	36.04 (2004)

2.2. Field Sampling Methods

To evaluate the efficacy of the treatments described by Keane and Parsons (2010) [3] for improving tree vigor, we established plots within the treatment units (control, prescribed burn, thinning, and both) and then selected saplings within these plots and extracted cross-sectional samples (increment cores or stem cookies) from the saplings. Plot locations were selected at random from a grid of points overlaid on the unit and located with a global positioning system (GPS) unit. Once the plot center was located by the field crew, a fixed area 0.04 ha circular plot was established. North and east photos were taken from plot center to provide a visual description of the plot. FFI methods [35] for measuring plot and tree characteristics were used to collect plot specific information. Universal Transverse Mercator (UTM) coordinates, elevation (m), landform, aspect, slope, ground cover, and habitat type [5] of each plot were recorded. The height, DBH, and status (healthy, unhealthy, sick, dead) of all trees (>11.4 cm DBH) within the plot boundary were also collected. The same information was collected for all of the saplings on the plot (trees < 11.4 cm DBH). Seedlings (trees < 1.37 m in height) were tallied by species and height class on a nested fixed area 0.004 ha plot using the same plot center as the 0.04 ha plot.

We selected one to four sample sapling trees from within the 0.04 ha plot. These trees were growing on the plot before the treatments occurred. The sample trees were selected by diameter class (four DBH classes) and health/vigor ratings adapted from [36] ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) classifications (Table 2) to ensure that no particular size class or vigor group

was favored. Changes were made to the original tree classes to better fit the morphology of whitebark pine with guidance from Kipfer [37].

Table 2. Vigor ratings used to select sample trees. None of the sampled trees had signs of white pine blister rust or mountain pine beetle attacks. Classes were modified from the Keen (1943) rating system.

Vigor Classes	Class Descriptions
4—Full vigor	<p>Crown—Full vigorous crowns, with a live crown ratio of 55% or more, average width or wider with density average or better</p> <p>Foliage—Needles are average length or longer, dense clusters</p> <p>Position—Usually isolated or dominant, rarely codominant with regard to the other trees close by</p>
3—Good to fair vigor	<p>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</p> <p>Foliage—Needles average length, dense clusters</p> <p>Position—Usually codominant, but sometimes isolated or dominant, rarely intermediate</p>
2—Fair to poor vigor	<p>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</p> <p>Foliage—Needles are often short and thinly distributed, but of normal length and density when confined to top third of crown</p> <p>Position—Usually intermediate, sometimes codominant or suppressed, rarely isolated</p>
1—Very poor vigor	<p>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</p> <p>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</p> <p>Position—Usually suppressed or intermediate, but may occur in other positions if greatly reduced in vigor</p>

The height (m) and DBH (cm) of the tree was measured and the tree evaluated for the health and vigor rating. For trees ≥ 5 cm DBH, one increment core was removed from the base of the tree, perpendicular to the slope to avoid compression wood. Cores were placed in paper straws for storage and transport. Trees < 5 cm DBH were cut at the base of the tree, and five discs were removed: one from the base and the other four at evenly spaced intervals up the tree (only the base disc was evaluated in this study).

2.3. Laboratory Procedures

All recorded field data were entered into the appropriate FFI databases [36] along with individual photos of the trees measured at each plot. Cores and tree sections were sanded with a belt sander and then hand-polished, 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 Astra Blue dye, mounted on a slide, and rescanned. Cores were crossdated and annual radial growth measured using CooRecorder 7.8 (Cybis Elektronik & Data AB). We verified dating using CDendro (Cybis Elektronik & Data AB) and created chronology for each site (site specific series intercorrelation = 0.35–0.4; mean sensitivity = 0.3).

2.4. Data Analysis

We calculated the basal area (BA) of each tree using DBH and then summed to obtain a plot-level basal area estimate. We used the dplR package [38] in RStudio [39] to determine cross-sectional basal

area increments (BAI; $\text{mm}^2 \text{ year}^{-1}$) from the ring widths measured from the core or disc taken at the base of each tree (not breast-height) from the ring year of sampling back to the year of germination. We then used BAI measurements to calculate growth ratios (GRs), relating growth post-treatment to growth pre-treatment. GRs greater than 1.0 translate to an increase in growth after treatment, and GRs less than one correspond to a decrease in growth. GR was calculated by dividing the post-treatment 10-year BAI by the 10-year pre-treatment BAI. We used an analysis of covariance (ANCOVA) to explore factors that might influence radial growth response [39]. The importance of these factors and interactions were assessed at a significance level of 0.05. Two-sample *t*-tests were also conducted to evaluate differences between the average GRs of trees in the control areas and of 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 [40]. 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.

3. Results

In total, we sampled 93 trees with DBH < 23 cm from the control and treatment units of 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 (Table 3). 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 Snowbowl were on average the oldest, with a mean age of 108 years old (Table 3). The species composition of the four sites was dominated by subalpine fir and whitebark pine (in that order) on the control plots, and by whitebark pine, subalpine fir, and lodgepole pine in the treated units.

Table 3. Age (yrs) and basal diameter (BD; cm) characteristics of the trees in the control and treatment units at the four sites. *n* is the sample size from each site. Age range: youngest to oldest sample trees from the site. Mean age: average age of all trees from the site with standard deviation in parentheses. Median BD: median basal diameter (cm) of trees sampled. Mean control age: average age of the trees sampled in the control units, standard deviation in parentheses. Mean trt. age: average age of the trees sampled in the treatment units. Median BD was used rather than the mean due to the modest sample size at each site and the presence of large BD trees, which disproportionately raised the average BD of the site.

Site	n	Elevation (m)	Age Range (Years)	Mean Age (Year)	Median BD (cm)	Mean Age (Year) Control Units	Mean Age (Year) Treated Units
Bear Overlook	20	2088–2148	20–201	74.3 (37.9)	5.21	67.6 (15.2)	80.9 (52.0)
Beaver Ridge	20	2134–2149	24–113	61.3 (23.9)	4.32	58.3 (26.0)	65.6 (16.8)
Coyote Meadows	31	2377–2438	17–118	56.3 (29.7)	5.33	67.3 (32.5)	49.3 (26.3)
Snowbowl	22	2164–2195	40–269	108.4 (59.8)	11.05	125.9 (70.4)	83.0 (27.0)

All of the Keane and Parsons [3] long-term monitoring plots in the treatment and control showed a decrease in stand basal area between the pre-treatment and post-treatment measurements (Table 1). In the control units, the agent of mortality could not be determined, however, all tree species were affected equally. The long time interval between measurements (4–19 years) at the monitoring plots did not allow us to determine exactly when mortality occurred. After aging the sample trees, we found a positive correlation ($r = 0.55$) between tree basal diameter (BD) and age. The sample tree site distribution was heavily skewed towards the smaller trees.

The average annual BAI ($\text{mm}^2 \text{ year}^{-1}$) for whitebark pine trees varied by site and treatment (Table 4). At Bear Overlook, the average BAI before treatment in the control was $232.43 \text{ mm}^2 \text{ year}^{-1}$, and the average BAI of the thinned and burned unit was $204.05 \text{ mm}^2 \text{ year}^{-1}$. After the treatment, the average BAI of the control unit decreased to $209.98 \text{ mm}^2 \text{ year}^{-1}$, but the average BAI of the thinned

and burned unit increased to 277.07 mm² year⁻¹ (Table 4). The pattern was the same at Beaver Ridge, where the average BAI decreased in control units and increased in the treated units. 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 units at Snowbowl, though the decline was proportionally greater in the control unit (Table 4).

Table 4. Site, treatment, number of units, tree sample size (n), mean BAI (basal area increment; mm² year⁻¹) before and after treatment with standard deviation in parenthesis, mean growth ratio (GR), and standard deviation in parenthesis. ** = statistically significant difference at $p < 0.05$, GR greater than 1 indicates an increase in growth after treatment. GR less than 1 indicates a decrease in growth after treatment.

Site	Treatment	Units	n	Pre-BAI (mm ² year ⁻¹)	Post-BAI (mm ² year ⁻¹)	Mean GR
Bear Overlook	Control	1	10	232 (266)	209 (230)	1.09 (0.55)
	Thin-Burn	2	10	204 (482)	277 (454)	2.34 ** (1.63)
Beaver Ridge	Control	2	12	984 (468)	939 (928)	1.59 (1.76)
	Burn	2	8	335 (1862)	627 (1655)	2.49 (0.77)
Coyote Meadows	Control	2	12	574 (140)	648 (207)	1.44 (1.39)
	Burn	2	8	123 (1617)	225 (1806)	2.67 (0.79)
	Thin-Burn	1	11	903 (834)	1232 (832)	2.25 ** (0.48)
Snowbowl	Control	1	13	676 (735)	519 (730)	0.99 (0.46)
	Thin	1	9	545 (1183)	520 (560)	1.04 (0.59)
All Sites	Control	6	13	634 (1200)	594 (1017)	1.28 (0.64)
	Thin	1	9	545 (1183)	520 (560)	1.04 (0.46)
	Burn	4	8	490 (1258)	690 (1454)	2.50 (1.47)
	Thin-Burn	3	21	354 (542)	555 (734)	2.31 ** (1.36)

Within a site, the mean GR was greater (105–215%) for all of the treated units than the control units. Site-level *t*-tests indicated that units that were thinned and later burned (Coyote Meadows and Bear Overlook) had a significantly higher GR than controls ($p = 0.05$; Table 4). 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 Snowbowl showed almost no difference in GR between the treated unit and the control unit (Table 4).

GR varied greatly among trees and this variation could only be partially explained from measured tree, plot, and site factors (Table 5; overall model $R^2 = 0.53$). Two trees were identified as potential outliers in terms of GR: 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. Some of the variability in GR was attributable to treatment: in particular, ANCOVA results showed that sample trees in treatment units had higher GRs than those in control units ($p = 0.0009$; Table 5). In addition to treatment effects, tree age negatively impacted GR, albeit in a manner that varied by site (Table 5, Figure 1). In contrast, the aggregate basal area (BA) of the sample tree plots as measured in 2016–2017 did not influence GR ($p = 0.76$; Table 5).

Table 5. Analysis of covariance results for the growth ratio (GR) model based on all sample trees and variables collected from all plots (df = degrees of freedom; bolded variables significant at 0.05 level).

Factor	df	F-Value	p-Value
Site	3	6.78	0.09
Treatment	3	6.47	<0.05
Tree age at treatment	1	8.86	<0.05
Elevation	1	0.29	0.59
Tree vigor at time of sampling	1	0.33	0.57

Table 5. Cont.

Factor	df	F-Value	p-Value
Tree basal diameter at treatment	1	0.13	0.72
Plot basal area at time of sampling	1	0.09	0.76
Site × Treatment	2	0.13	0.87
Site × Tree age at treatment	3	3.33	<0.05
Site × Elevation	3	1.25	0.29
Site × Tree vigor at time of sampling	3	0.15	0.92
Site × Plot basal area at time of sampling	3	0.71	0.54
Site × Tree basal diameter at treatment	3	0.59	0.62

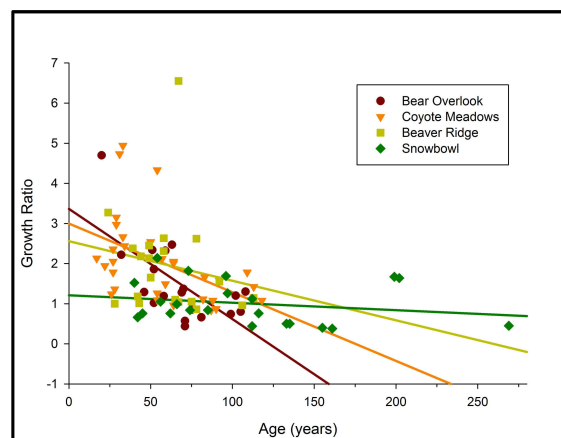


Figure 1. Relationship between growth ratio and tree age by site (CM: Coyote Meadows; SB: Snowbowl; BO: Bear Overlook; BR: Beaver Ridge).

4. Discussion

Given the rapid decline of whitebark pine throughout much of its range, and the expense of ecological restoration, questions about whether and how whitebark pine regeneration responds to treatments are crucial for future management of the species [28]. This study is the first to examine the radial response of whitebark regeneration to release treatments. The difficulties of accessing and locating healthy whitebark pine regeneration resulted in a modest sample size for this study. Overall, we found that restoration treatments increased tree vigor, as evidenced by increases in GR. However, the high variability in growth among trees in treated units as well as the lack of data on tree vigor or competition immediately post-treatment did not allow us to attribute this increase in growth to any single treatment factor.

A previous study found similar results in mature whitebark pine. Keane et al. [34] examined stem cross-sections from 59 mature whitebark pine sampled from 21 logged stands where most of the competing tree species were removed by logging activity and not as part of a restoration treatment. Of all the trees sampled, 14 were excluded from analysis because they did not have enough rings to calculate pre-logging growth. Of the remaining trees, more than 80% showed an increase in radial growth. Similar to this study, 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 ruled out as the cause for the increased ring width because the year-to-year growth trends did not correlate with these climate variables [34]. Some trees immediately increased their radial growth after logging, while others experienced a lag of up to 15 years before they showed any response to the treatment. The few saplings included in the study decreased in radial growth immediately after treatment. This was attributed to a lack of established root systems and foliage to support the sudden increase in available resources. Our findings are consistent with those of Keane et al. [34] in regard to increased

radial growth in treated stands post-harvest. Our study found that younger trees tended to show a greater increase in GR than did older ones, possibly due to the plasticity of key traits such as root development and leaf morphology, which may be linked to tree vigor, but this was unable to be determined in this study (Table 4, Figure 1). This highlights the fact that diameter is not a good surrogate for age—some of our saplings were over 100 years old—and suggests that once whitebark trees in the understory reach an advanced age they may respond slowly or poorly to release treatments.

Aggregate basal area did not affect GR. 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 (variation among sites is absorbed by the site factor variable). Interestingly, vigor class of the sample trees—as measured in 2016–2017—also did not influence GR. 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.

An unexpected issue that we encountered during the study was the high amount of tree mortality occurring in the control units post-treatment (Figure 2). In the treated units, the reduction in stand basal area was assumed to occur mostly around the time of treatment. However, in the control units, considerable mortality for all species occurred over time. We assessed the causes of mortality as drought stress, spruce budworm (*Choristoneura fumiferana* Clemens), and non-specific fir die-off in the subalpine fir and spruce, and white pine blister rust and mountain pine beetle in both pines. Since this mortality occurred gradually, we assumed trees in control units are also likely experiencing a reduction in competition and concomitant slow release because of the high mortality. While this complicates assessment of the direct treatment impacts on GR, it suggests our treatment comparisons of GR are conservative and differences in controls without mortality could be expected to be even more pronounced.

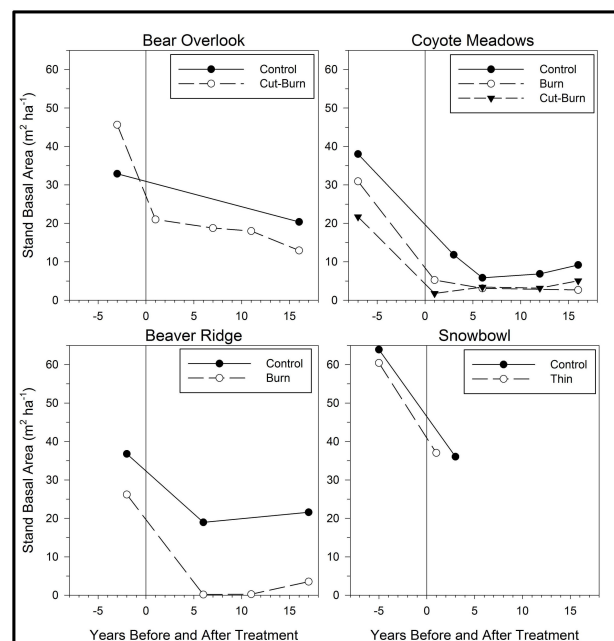


Figure 2. Changes in stand basal area ($\text{m}^2 \text{ha}^{-1}$; live trees above 11.3 cm diameter at breast height (DBH)) observed in the long-term monitoring plots across the four study sites (CM: Coyote Meadows; SB: Snowbowl; BO: Bear Overlook; BR: Beaver Ridge). The vertical line (year 0) indicates when treatment occurred.

We focused specifically on average ring growth 10 years pre- and post-treatment. Due to this relatively short time window, we were unable to fully examine the duration of the release that the trees may experience. Some of the trees in the study by Keane et al. [34] still showed positive ring width responses up to 20 years after the harvest. Additionally, other trees experienced lag times of up to 15 years before responding to the release treatment. The narrow window of time after treatments (15 years) we studied may be insufficient for determining how long the whitebark saplings respond to treatment. It also constrains the ability to determine if trees that had no 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.

The universally high variability in GR among trees in this study was only partially attributed to measured site and tree factors ($R^2 = 0.53$). The unexplained portion could be due to a variety of unmeasured factors such as variations in microsite, competition, or exposure. Notably, the variability between trees in the control area was less than that of the treated areas except at Snowbowl (Table 4). In the control sites, the basal areas of the plots were fairly similar plot to plot [3], and there was also less variability in the GR of the trees. In the treatment units, the basal area of the plots varied greatly [3] and there was more variability in the GR of the sample trees. Because we did not measure neighborhood competition from other trees within and outside a plot, our models were unable to determine if this affected GR (Figure 3).

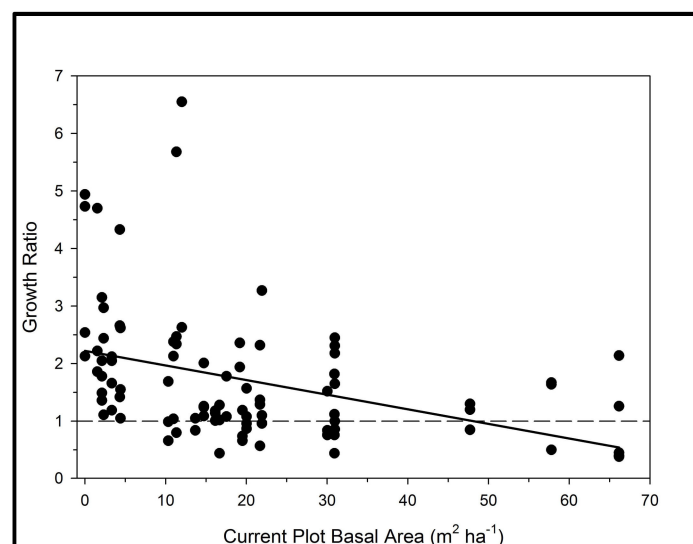


Figure 3. Relationship between growth ratio and plot basal area for all sample trees.

Limiting factors such as nutrients, water, snowpack, or light, can change how a tree responds to changes in the environment [41]. It may be that some of the younger, smaller sample trees were limited by nutrients or competition effects reducing 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 may have more developed crowns and, presumably, more extensive root systems, and therefore may be less reactive to site-specific seasonal variation, resulting in smaller variations in GR [41]. Furthermore, some of the variability observed in GR may be due to tree genetics. Liu et al. [42] found clear genetic differentiation among seed families and spatial patterns of several genetic subgroups of whitebark pine. In addition to genetic variation, some of the variability between individual trees may be traced back to the seed source. Leirfallom et al. [10] 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.

5. Restoration and Management Implications

Despite the difficulties of restoring high-elevation ecosystems, managers are beginning to implement treatments that aim to mimic historical disturbance regimes in whitebark pine stands [3]. Whitebark pine has a competitive advantage until more shade-tolerant species begin to out-compete the species [3]. With continued suppression of wildfire in whitebark pine environments, managers may need to rely on silvicultural cuttings and prescribed fire as a means of restoring whitebark pine to the landscape. These treatments are usually used in late seral 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 [34]. Results from this study show that thinning and prescribed burning treatments can indeed increase tree growth (Table 4) and hopefully enhance future cone crops.

The study sites for this project are part of an on-going restoration project, established in the mid-1990s, which applied a mix of silvicultural treatments and prescribed burns to five whitebark sites in the Bitterroot Range of Montana, USA, to examine the outcome of restoring whitebark pine ecosystems to historic stand structures. Ten-year results from Keane and Parsons [3] show that whitebark pine presence is increasing in these treated areas. There is also a low prevalence of white pine blister rust in new seedlings and little to no signs of mountain pine beetle attack in mature trees [3]. The main drawbacks of restoration efforts like these are that they are 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 advanced-aged whitebark regeneration responds to treatments, add additional evidence that whitebark pine saplings can respond to a variety of restoration methods.

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References

1. Ellison, A.M.B.; Bank, M.S.; Clinton, B.D.; Colburn, E.A.; Elliott, K.; Ford, C.R.; Foster, D.R.; Kloeppel, B.D.; Knoepp, J.D.; Lovett, G.M.; et al. Loss of Foundation Species: Consequences for the Structure and Dynamics of Forested Ecosystems. *Front. Ecol. Environ.* **2005**, *3*, 479–486. [[CrossRef](#)]
2. Tomback, D.F.; Achuff, P. Blister Rust and Western Forest Biodiversity: Ecology, Values and Outlook for White Pines. *For. Pathol.* **2010**, *40*, 186–225. [[CrossRef](#)]
3. Keane, R.E.; Parsons, R.A. *A Management Guide to Ecosystem Restoration Treatments: Whitebark Pine Forests of the Northern Rocky Mountains*; USDA Forest Service Rocky Mountain Research Station: Fort Collins, CO, USA, 2010.
4. Tomback, D.F. Dispersal of Whitebark Pine Seeds by Clark's Nutcracker: A Mutualism Hypothesis. *J. Ecol.* **1982**, *51*, 451–467. [[CrossRef](#)]
5. Arno, S.F.; Hoff, J.R. *Silvics of Whitebark Pine (Pinus albicaulis)*; General Technical Report INT; USDA Forest Service: Washington, DC, USA, 1989; pp. 253–264.
6. Kendall, K.C. Bear Squirrel Pine Nut Interaction. In *Annual Report 1978–1979. Yellowstone Grizzly Bear Investigations*; USDI National Park Service: West Glacier, MT, USA, 1980; pp. 51–60.

7. Lorenz, T.J.; Aubry, C.; Shoal, R. *A Review of the Literature on Seed Fate in Whitebark Pine and the Life History Traits of Clark's Nutcracker and Pine Squirrels*; General Technical Report PNW-GTR; USDA Forest Service Pacific Northwest Research Station: Portland, OR, USA, 2008; p. 742.
8. Morgan, P.; Bunting, S.C.; Keane, R.E.; Arno, S.F. Fire Ecology of Whitebark Pine (*Pinus albicaulis*) Forests in the Rocky Mountains, USA. In *Proceedings of the International Symposium Subalpine Stone Pines and Their Environment: The Status of Our Knowledge*; St. Moritz, Switzerland, 5–11 September 1992, General Technical Report INT-GTR; Schmidt, W.C., Holtzmeier, F.-K., Eds.; USDA Forest Service, Intermountain Research Station: Ogden, UT, USA, 1994; Volume 309, pp. 136–142.
9. Arno, S.F.; Weaver, T. *Whitebark Pine Community Types and Their Patterns on the Landscape*; General Technical Report INT; USDA Forest Service: Bozeman, MT, USA, 1990; p. 270.
10. Leirfallom, S.B.; Keane, R.E.; Tomback, D.F.; Dobrowski, S.Z. The Effects of Seed Source Health on Whitebark Pine (*Pinus albicaulis*) Regeneration Density after Wildfire. *Can. J. For. Res.* **2015**, *45*, 1597–1606. [[CrossRef](#)]
11. Callaway, R.M. Competition and Facilitation on Elevation Gradients in Subalpine Forests of the Northern Rocky Mountains, USA. *OIKOS* **1998**, *82*, 561–573. [[CrossRef](#)]
12. Resler, L.M.; Tomback, D.F. Blister Rust Prevalence in Krummholz Whitebark Pine: Implications for Treeline Dynamics, Northern Rocky Mountains, Montana, USA. *Arct. Antarct. Alp. Res.* **2008**, *40*, 161–170. [[CrossRef](#)]
13. Bingham, R.T. Taxonomy, Crossability, and Relative Blister Rust Resistance of 5 Needled White Pines. In *Biology of Rust Resistance in Forest Trees*; USDA Miscellaneous Publication: Ogden, UT, USA, 1972; Volume 1221, pp. 271–280.
14. Hoff, R.; Bingham, R.T.; Macdonald, G.I. Relative Blister Rust Resistance of White Pines. *Eur. J. For. Pathol.* **1980**, *10*, 11–17. [[CrossRef](#)]
15. Maloy, O.C. A Case History of Whitepine Blister Rust Control in North America. *Annu. Rev. Phytopathol.* **1997**, *35*, 87–109. [[CrossRef](#)] [[PubMed](#)]
16. McKinney, S.T.; Tomback, D.F. The Influence of White Pine Blister Rust on Seed Dispersal in Whitebark Pine. *Can. J. For. Res.* **2007**, *37*, 1044–1057. [[CrossRef](#)]
17. Schwandt, J.W.; Lockman, I.B.; Kliejunas, J.T.; Muir, J.A. Current Health Issues and Management Strategies for White Pines in the Western United States and Canada. *For. Pathol.* **2010**, *40*, 226–250. [[CrossRef](#)]
18. Wood, D.L. The Bark and Ambrosia Beetles of North and Central American (Coleoptera: Scolytidae), a Taxonomic Monograph. In *Great Basin Naturalist Memoirs*; Brigham Young University: Provo, UT, USA, 1982.
19. Dooley, E.M.; Six, D.L.; Powell, J.A. A Comparison of Mountain Pine Beetle (Coleoptera: Curculionidae, Scolytinae) Productivity and Survival in Lodgepole and Whitebark Pine after a Region-Wide Cold Weather Event. *For. Sci.* **2015**, *61*, 235–246. [[CrossRef](#)]
20. Logan, J.A.; Powell, J.A. Ghost Forests, Global Warming, and the Mountain Pine Beetle (Coleoptera: Scolytidae). *Am. Entomol.* **2001**, *47*, 160. [[CrossRef](#)]
21. Macfarlane, W.W.; Logan, J.A.; Kern, W.R. An Innovative Aerial Assessment of Greater Yellowstone Ecosystem Mountain Pine Beetle-Caused Whitebark Pine Mortality. *Ecol. Appl.* **2013**, *23*, 421–437. [[CrossRef](#)] [[PubMed](#)]
22. Brown, J.K.; Arno, S.F.; Barrett, S.W.; Menakis, J.P. Comparing the Prescribed Natural Fire Program with Presettlement Fires in the Selway? Bitterroot Wilderness. *Int. J. Wildland Fire* **1994**, *4*, 157–168. [[CrossRef](#)]
23. Keane, R.E.; Morgan, P.; Menakis, J.P. Landscape Assessment of the Decline of Whitebark Pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. *Northwest Sci.* **1994**, *68*, 213–229.
24. Schaming, T.D. Population-Wide Failure to breed in the Clark's Nutcracker (*Nucifraga columbiana*). *PLoS ONE* **2015**, *10*, e0123917. [[CrossRef](#)] [[PubMed](#)]
25. Keane, R.E.; Arno, S.F.; Stewart, C.A. Ecosystem-Based Management in the Whitebark Pine Zone. In *Proceedings of the Bitterroot Ecosystem Management Research Project: What We Have Learned*, Missoula, MB, Canadian, 18–20 May 2000; pp. 36–40.
26. Service, US Fish and Wildlife. Endangered and Threatened Wildlife and Plants, 12-Month Finding on a Petition to List *Pinus albicaulis* as Endangered or Threatened with Critical Habitat. *Fed. Regist.* **2011**, *76*, 42631–42654.
27. Government of Canada. Order Amending Schedule 1 to the Species at Risk Act. In *Can. Gaz. Part II*; Government of Canada: Ottawa, ON, Canada, 2012; Volume 145, pp. 103–135.
28. Keane, R.E.; Holsinger, L.M.; Mahalovich, M.F.; Tomback, D.F. *Restoring Whitebark Pine Ecosystems in the Face of Climate Change*; USDA Forest Service Rocky Mountain Research Station: Fort Collins, CO, USA, 2017.
29. Keane, R.E.; Parsons, R.A. Restoring Whitebark Pine Forests of the Northern Rocky Mountains, USA. *Ecol. Restor.* **2010**, *28*, 56–70. [[CrossRef](#)]

30. Keane, R.E.; Tomback, D.F.; Aubry, C.A.; Bower, A.D.; Campbell, E.M.; Cripps, C.L.; Jenkins, M.B.; Mahalovich, M.F.; Manning, M.; McKinney, S.T.; et al. *A Range-Wide Restoration Strategy for Whitebark Pine Forests*; USDA Forest Service Rocky Mountain Research Station: Fort Collins, CO, USA, 2012.
31. Brockwell, P.J.; Davis, R.A. *Introduction to Time Series*; Springer: New York, NY, USA, 2002.
32. Silviculture Instructors Subgroup. *Silviculture Working Group (D2) Society of American Foresters*; Terminology Committee, Silviculture Technology: Bethesda, MD, USA, 1994; Available online: http://oak.snr.missouri.edu/silviculture/silviculture_terminology.htm (accessed on 31 May 2018).
33. Arno, S.F. Whitebark Pine Crops: A Diminishing Source of Wildlife Food. *West. J. Appl. For.* **1986**, *1*, 92–95.
34. Keane, R.E.; Gray, K.L.; Dickinson, L.J. *Whitebark Pine Diameter Growth Response to Removal of Competition*; U.S. Department of Agriculture Forest Service Rocky Mountain Research Station: Fort Collins, CO, USA, 2007; 32p.
35. Lutes, D.C.; Benson, N.C.; Keifer, M.; Caratti, J.F.; Streetman, A.S. FFI: A Software Tool for Ecological Monitoring. *Int. J. Wildland Fire* **2009**, *18*, 310–314. [[CrossRef](#)]
36. Keen, F.P. Ponderosa Pine Tree Classes Redefined. *J. For.* **1943**, *41*, 249–253.
37. Kipfer, T.R. Post-Logging Stand Characteristics and Crown Development of Whitebark Pine (*Pinus albicaulis*). Ph.D. Thesis, Montana State University, Bozeman, MT, USA, 1992.
38. Bunn, A.G. A Dendrochronology Program Library in R (Dplr). *Dendrochronologia* **2008**, *26*, 115–124. [[CrossRef](#)]
39. RC Team. R: A Language and Environment for Statistical Computing. Available online: <ftp://164.41.45.44/pub/plan/R/web/packages/dplr/vignettes/timeseries-dplr.pdf> (accessed on 31 May 2018).
40. Tukey, J.W. *Exploratory Data Analysis*; Addison-Wesley: Reading, MA, USA, 1977.
41. Poorter, H.; Nagel, O. The Role of Biomass Allocation in the Growth Response of Plants to Different Levels of Light, CO₂, Nutrients, and Water: A Quantitative Review. *Australian. J. Plant Physiol.* **2000**, *27*, 495–507.
42. Liu, J.J.; Snieszko, R.; Murry, M.; Wang, N.; Chen, H.; Zamany, A.; Sturrock, R.N.; Savin, D.; Kegley, A. Genetic Diversity and Population Structure of Whitebark Pine (*Pinus albicaulis* Engelm.) in Western North America. *PLoS ONE* **2016**, *11*, e0167986. [[CrossRef](#)] [[PubMed](#)]



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