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ARTICLE

Vegetation Ecology

Thinning enhances whitebark pine (*Pinus albicaulis*) growth and resin duct defenses

Nickolas E. Kichas[1,2] | **Erin K. Shanahan**[3] | **Sharon M. Hood**[4]

[1]National Park Service, Yellowstone National Park, Wyoming, USA

[2]U. S. Department of Energy, Oak Ridge Institute for Science and Education, Oak Ridge, Tennessee, USA

[3]National Park Service, Northern Rocky Mountain Science Center, Bozeman, Montana, USA

[4]U.S. Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA

Correspondence
Nickolas E. Kichas
Email: nickolas_kichas@nps.gov

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Abstract

Whitebark pine (*Pinus albicaulis*) is an important component of high-elevation ecosystems throughout the northern Rocky Mountains; however, the species was recently listed as "threatened" under the Endangered Species Act due to widespread mortality throughout its native range. Land managers tasked with whitebark pine conservation and restoration require information on strategies that can positively influence whitebark pine establishment and promote growth and defense of preexisting trees on the landscape. Our study investigated the response of whitebark pine tree growth and resin duct defenses to thinning and removal of competing shade-tolerant conifers in the Caribou-Targhee National Forest, Idaho, USA. In the nine years following thinning treatments, we found that whitebark pine trees (>12.7 cm diameter at breast height [dbh]) responded favorably to thinning and experienced a 60% increase in basal area increment (52% increase in ring width index) while also producing 34% more resin ducts. Additionally, resin ducts were 23% larger with 49% increased area in the nine years post-thinning compared with trees in the control. Small diameter (<5 cm dbh) whitebark pine in the treatment experienced a dramatic growth release with over 90% increase in basal area increment (74% increase in ring width index). Thinning also created conditions favorable for whitebark pine seedling and sapling establishment. In the treatment, 75% of seedlings and 93% of saplings were whitebark pine, compared with 32% seedlings and 14% saplings in the control. In addition, 93% of overstory trees in the treatment were whitebark pine, compared with 42% in the control. Whitebark pine tree mortality was similar across both the control (26%) and the treatment (25%), indicating that the thinning treatments did not have any adverse impacts on tree mortality. The positive effects of thinning on whitebark pine establishment and tree growth, coupled with the lack of elevated mortality in the treatment, provide strong evidence in support of thinning as a viable silvicultural technique in whitebark pine conservation efforts.

KEYWORDS
competition, defense, growth response, resin ducts, thinning, whitebark pine

INTRODUCTION

Whitebark pine (*Pinus albicaulis*) is an important component of high-elevation ecosystems throughout the northern Rocky Mountains, USA. Whitebark pine trees provide numerous ecological benefits, including stabilizing erosive slopes, promoting vegetative establishment in subalpine environments, increasing snow retention, and promoting snowpack development (Tomback et al., 2001). Whitebark pine seeds are also highly nutritious and an important food source for a variety of wildlife. However, whitebark pine forests have experienced increased mortality, particularly over the past century due to cumulative impacts of native mountain pine beetle (*Dendroctonus ponderosae*), altered fire regimes, successional replacement by competing conifers, and the nonnative pathogen white pine blister rust (*Cronartium ribicola*), which has caused significant mortality (>90%) in some stands (Keane & Arno, 1993; Kendall & Keane, 2000; Tomback et al., 2001). These factors, along with unfavorable projections for future whitebark pine establishment under a changing climate (Chang et al., 2014), collectively led the U.S. Fish & Wildlife Service to formally list the species as "threatened" under the Endangered Species Act. Given the multiple threats to whitebark pine, understanding whitebark pine population demographics and developing strategies to promote whitebark pine tree health are essential in maintaining this threatened species across the landscape (Keane et al., 2017; Tomback et al., 2022).

To maintain and restore whitebark pine forests, agencies and land managers require information on the response of whitebark pine trees to various management activities. In the Greater Yellowstone Ecosystem (GYE), restoration treatment alternatives and monitoring of regeneration dynamics have been identified as important research needs (GYCC, 2011). Monitoring the establishment and growth of whitebark pine following changes in stand dynamics provides the best measure of management action success (Tomback et al., 2022). While thinning treatments and silvicultural cuttings are common restoration methods used to reduce competition around desirable trees, data documenting the impacts of these practices on whitebark pine growth are sparse (Keane, 2018; Retzlaff et al., 2018), and studies examining effects on tree defenses to bark beetles (e.g., resin duct characteristics) are nonexistent. This, in part, is due to the topographically complex, high-elevation environments where whitebark pine trees grow, which can complicate both large- and small-scale management activities (Keane, 2000; Tomback, 2001). In one study, Keane et al. (2007) found that timber harvesting treatments aimed at reducing whitebark pine competition facilitated a growth release, most notably in older, larger trees as well as in stands with greater preharvest densities (Keane et al., 2007). Similarly, Retzlaff et al. (2018) found potential for smaller whitebark pine trees to release after thinning and prescribed fire treatments, although this effect depended on tree age, with younger trees experiencing a greater release in growth than older trees (Retzlaff et al., 2018).

While restoration of whitebark pine communities has been recognized as a critical element in mitigating whitebark pine decline, restorative treatments aimed at promoting whitebark pine growth and establishment have had mixed success, particularly given the species unique relationships to fire, insects, pathogens, and climate (Keane, 2018; Keane et al., 2013, 2017; Millar et al., 2015; Millar & Delany, 2019; Tomback et al., 2001, 2022). For instance, Keane and Parsons (2010) found that while prescribed fire promoted conditions conducive to seed caching by whitebark pine's primary seed distributer, Clark's nutcracker (*Nucifraga columbiana*), fire also increased mortality of seemingly healthy whitebark pine trees. In addition, the silvicultural treatments increased fuel loadings, further reducing caching habitat and limiting potential for new seedling establishment (Keane & Parsons, 2010). Maher et al. (2018) also found mixed results with restoration treatments that depended in part on the condition of the stand pretreatment (e.g., closed-canopy versus open park-like stands), with the most notable growth release occurring in the closed-canopy stand. The nuanced response of whitebark pine to such treatments reflects the unique ecology of this long-lived species and warrants further research across a broad range of biogeographic environments to better understand the potential for success in management activities across diverse whitebark pine habitat.

The goals of this project are to investigate (1) physiological responses of whitebark pine trees and (2) regeneration responses to mechanical thinning of competing shade-tolerant conifers in eastern Idaho, USA. We use tree-ring analysis to evaluate growth and resin duct responses of whitebark pine to mechanical thinning treatments. Our study is the first to investigate the impacts of thinning on whitebark pine resin duct defenses. Examining resin duct characteristics is important in whitebark pine, and other conifers, because defense characteristics play a crucial role in moderating bark beetle interactions, with trees persisting through bark beetle outbreaks often exhibiting distinct resin duct characteristics (Ferrenberg et al., 2014; Hood et al., 2015; Hood & Sala, 2015; Kane & Kolb, 2010; Kichas et al., 2020). This is especially relevant in whitebark pine habitats due to endemic beetle pressures and frequent potential for eruptive bark beetle outbreaks that could influence the success of restoration treatments (Keane & Parsons, 2010; Kichas et al., 2020; Maher et al., 2018; Retzlaff et al., 2018). Additionally, understanding the effects of thinning on whitebark pine mortality and regeneration is critical for developing successful restoration techniques.

We hypothesize that thinning treatments will positively influence both tree growth and defense of residual whitebark pine trees, due primarily to decreased competition and increased availability of resources conducive to carbohydrate accumulation benefiting both tree growth and defense. We further suspect that whitebark pine trees are responding favorably to growing season temperature, characterized by the high-elevation, energy-limited systems in which these trees grow (Kichas et al., 2023) and that thinning will increase whitebark pine regeneration via increased light availability. Our results are of interest to land managers and practitioners who are tasked with supporting strategies to enhance whitebark pine vigor and establishment across multiple jurisdictions. Given that silvicultural thinning is a prescribed tool for whitebark pine restoration across much of its range (GYCC, 2011; Tomback et al., 2022), our findings will provide direct evidence for evaluating this management treatment aimed at promoting whitebark pine health and vigor.

MATERIALS AND METHODS

Site description and thinning treatments

Data for this study were collected across four high-elevation whitebark pine units (two control and two treatment units) located to the southeast of Sawtell Peak on the Caribou-Targhee National Forest in eastern Idaho (Appendix S1: Figure S1). The study area sits at approximately 2710 m above sea level (asl) and experiences mean annual temperatures of 2.8°C with around 700-mm annual rainfall, which occurs primarily as snowfall from November through April. These high-elevation montane forests are predominately comprised of whitebark pine, subalpine fir (*Abies lasiocarpa*), and Engelman spruce (*Picea engelmannii*) with a small component of lodgepole pine (*Pinus contorta*).

In the spring of 1999, 2000, and 2002, the ~16-ha treatment areas were mechanically thinned to remove whitebark pine competitors (predominately subalpine fir). This unit was selected for thinning due to the density of whitebark pine in both the overstory and understory, logistical practicalities, and its proximity to a well-established road. As part of these treatments, all non-whitebark pine trees >20 cm diameter at breast height (dbh) were mechanically girdled, while trees <20 cm dbh were felled or hand pulled in an effort to reduce competition and create forest openings conducive to whitebark pine regeneration. An untreated control unit was established approximately 0.6 km to the south of the treated areas. The control unit had no obvious signs of differing stand or disturbance histories and was situated geographically close to the treatment areas to reduce potential microsite variability that could otherwise influence whitebark pine growth and establishment. In 2010, 2011, and 2012, the U.S. Forest Service applied verbenone patches to live, healthy whitebark pine trees across the treatment and control areas to reduce mountain pine beetle activity and limit insect-related mortality for the broader region. In 2012, all subalpine fir <20 cm were pulled or cut a second time from the thinned unit. For statistical analyses and reporting purposes, we combined data from the two thinned areas and two control areas, respectively (Appendix S1: Figure S1).

Data collection

In September 2014, 91 healthy, live whitebark pine trees between 10 and 25 cm dbh were sampled across the treatment and control. We sampled trees visibly free from symptoms of white pine blister rust (blister rust), mechanical damage, or visibly distorted growth forms. We chose trees within the 10–25-cm diameter class because we were primarily interested in the effects of the 1999–2002 thinning treatments and speculated that trees experiencing the greatest effects in terms of growth release would grow into this size class in the 10 years following treatment. While mountain pine beetle attack pines >10 cm dbh, when available, they preferentially select trees >20–25 cm dbh (Gibson et al., 2009; Safranyik & Carroll, 2006). Our sampling investigated the effects of thinning on sub-host sized trees to see if the treatment increased growth and resin duct defenses to improve the likelihood and timeliness that smaller whitebark pines would grow into mature cone-bearing trees.

We collected two increment cores from each tree (176 cores total, with 94 cores from 49 trees in the control and 82 cores from 42 trees in the treatment). At each tree, a detailed description of tree health and growth form was recorded, as well as blister rust infection status (number of cankers, location of cankers on branches or bole, and whether infections were active or inactive) and whether trees were growing as individual stems or in clumps/groups. At every fifth tree, a 15.24 × 0.9 m belt transect was established on a randomly selected azimuth to quantify understory recruitment and basal area.

We also collected one increment core from six overstory trees of whitebark pine and other species across the control and treatment and recorded competition (species and dbh data for live and dead trees) around these individuals using a basal area factor 20 angle gauge. In addition, a total of 20 small diameter whitebark pine trees (dbh ranging from 2 to 5 cm) in the treatment were destructively sampled to assess whether the thinning treatments had any impact on growth of trees in this smaller size class.

In the summer of 2023, the stands were visited again to assess mortality and regeneration across both the treatment and control. In our 2023 site surveys, we established 14 permanent monitoring plots; seven plots in the control and seven plots in the treatment (Appendix S1: Figure S1). In each of the monitoring plots, we tallied whitebark pine and non-whitebark pine seedlings (trees <1.38-m tall) by height class in 0.004-ha circular plots (plot radius of 3.6 m), and saplings (≥1.2-m tall and <12.7 cm dbh) in 0.02-ha circular plots (plot radius of 8 m). Additionally, we measured all trees (>12.7 cm dbh) in 0.04-ha circular plots (plot radius of 11.3 m). We also documented symptoms of blister rust infection for all live whitebark pine trees in both the treatment and control.

Sample preparation

Increment cores and small diameter cross sections that were collected in the 2014 field campaign were air-dried, prepared and processed using standard dendrochronological techniques (Cook & Kairiukstis, 1990; Stokes & Smiley, 1996). Ring widths were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with the recording software Measure J2X (Voortech Consulting, 2005). Tree-ring series were cross-dated visually and graphically using ring width patterns and frost rings and were statistically checked using COFECHA (Holmes et al., 1986).

To assess the influence of thinning treatments on resin duct anatomy, we scanned individual tree cores at high resolution (1200 dpi; 472 pixels/cm) on an Epson V550 flatbed scanner and measured resin duct features using the program ImageJ (version 1.46r, National Institutes of Health, Bethesda, MD, USA). All resin ducts were measured to the nearest 1×10^{-7} mm^2 using the ellipse tool and the calendar year in which they formed was documented. For resin duct metrics, we followed established methods (Hood et al., 2020; Hood & Sala, 2015) and collected measurements across five categories, including non-relativized measures of resin duct size (mean size of all resin ducts per annual ring; in square millimeters), duct production (number of ducts per year), and total duct area (sum of resin duct size: in square millimeters per year), as well as resin duct measures that have been relativized to ring area, including duct density (number of resin ducts per square millimeters per year) and relative duct area (% annual ring). We measured ring widths for the small (2–5 cm) diameter trees but did not assess resin duct characteristics.

We also investigated the degree to which climate modulated growth and defense characteristics in whitebark pine and whether there were detectable differences in the response of trees sampled in the control and treatment to seasonal changes in climate. We obtained estimates of local climate within the study area from the Parameter-elevation Regressions on Independent Slopes Model (PRISM), as instrumental weather data were not available at these sites (Abatzoglou et al., 2017; Daly et al., 1994; Kipfmueller & Salzer, 2010). Monthly climate variables obtained for this analysis included temperature (minimum, maximum, and average), precipitation, and vapor pressure deficit (VPD). PRISM data were obtained at a spatial resolution of 4 km using the AN (daily and monthly) version of the dataset (Abatzoglou et al., 2017). We opted to use this version of the PRISM dataset because: (1) it is freely and publicly available, (2) it is reasonably accurate, given the sparse network of instrumental stations across our broader study region, and (3) it is a commonly utilized dataset for many dendroecological studies, particularly in high-elevation areas with complex topography [e.g., Ferrenberg et al., 2017; Goeking et al., 2018; Guiterman et al., 2015; Kipfmueller & Salzer, 2010]).

We grouped monthly climate data into annual and seasonal windows to evaluate the more nuanced response of trees to seasonal variability. For temperature records, "warm season" encompasses May through September, "Spring" includes March through May, while "Summer" includes June through August. For precipitation, we also considered "cool season," which encompasses October (from the previous year) through April, and "water year," which is a metric characterizing surface-water supply over a 12-month period, from October (of the previous year) through September. This is relevant in these high-elevation environments with complex topography where moisture can persist annually.

Data analysis

All analyses were conducted using the statistical package R (version 4.3.0) (R Development Core Team, 2008). We utilized correlation, analysis of variance (ANOVA), multivariate analyses, and *t*-test analyses to examine relationships between growth and defense across the control and treatment, as well as between trees that grew as individual stems versus those in clumps/groups. To investigate the influence of the thinning treatments on tree growth and resin duct morphology, we calculated a ratio of growth and resin duct metrics as the average difference between the nine years prior to treatment (1990–1998) and nine years following the 1999–2002 thinning treatments (2003–2011). For growth measures, we utilized basal area increment (BAI; in square centimeters per year), which was calculated using the *bai.out* function in the dplR package (version 1.75) (Bunn, 2008). We also utilized a standardized, unitless ring width index (RWI), which was developed through interactive detrending using the *i. detrend* function in the dplR package. For the RWI, each tree-ring series was individually fit with a negative exponential curve or a flexible spline with a frequency response of 75% of the series length to remove the geometric growth trend (Fritts, 1976). Each tree-ring series was then divided by the fitted trend line, resulting in a standardized, unitless ratio (index) of actual to expected values (Cook & Peters, 1997). We utilized conservative detrending options to preserve multi-decadal variability within the ring width series, as this was assumed to reflect possible important climate and ecological interactions, such as response to pests, pathogens, and stand dynamics that could influence growth suppressions and releases. Climate analyses were conducted using the detrended RWI series and the *seascorr* and *dcc* functions in the treeclim package (version 2.0.6), as well as the *monthly_response_seascorr* function in the dendroTools package (version 1.2.10).

Although observed blister rust occurrence was relatively low across the control and treatment in 2014, we identified seven pairs of trees with and without blister rust symptoms (seven diseased trees and seven disease-free trees of similar size). We considered a tree to be diseased only when aecia were present or three of five blister rust indicators (flagging, rodent chewing, roughened bark, swelling, oozing sap) in the same exact location on either the tree bole or branches. We paired trees based on diameter (<0.5 cm difference) to control for potential differences in growth form and looked for differences in growth and resin duct anatomy to see if blister rust had a notable impact on tree growth and resin duct morphology. Lastly, we summed basal area (in square meters) from the overstory trees, as well as from the belt transect data collected from every 5th tree in the 2014 field sampling campaign. From this competition data, we calculated the metric stand density index (SDI) (Reineke, 1933) around 19 trees (11 trees in the control and 8 trees in the treatment) and evaluated relationships between SDI and whitebark pine growth and resin duct defenses.

RESULTS

Stand-level regeneration and mortality

In 2023, 75% of seedlings (trees <1.38-m tall) in the thinning treatment were whitebark pine compared with 32% in the control ($F = 3.22$, $p = 0.046$). In the treatment, whitebark pine seedling abundance was marginally higher in the smallest and largest height class (Table 1). For non-whitebark pine seedlings, we found significantly lower levels in the smallest ($p = 0.011$) and largest ($p = 0.031$) height classes in the treatment and moderately lower levels in the intermediate height classes (Table 1). For saplings (trees ≥1.2-m tall and <12.7 cm dbh), 93% were whitebark in the treatment compared with 14% in the control ($F = 18.2$, $p < 0.001$). Whitebark pine sapling abundance was relatively similar between the control and treatment, with slightly higher abundance in the control for the smallest and largest diameter classes (Table 1). There were significantly fewer non-whitebark pine saplings in the treatment in the small and intermediate size classes (<2.54–7.62 cm dbh) and moderately fewer in the largest diameter classes (Table 1). For overstory trees (>12.7 cm dbh), 93% were whitebark pine in the treatment compared with 42% in the control ($F = 46.8$, $p < 0.001$). Whitebark pine tree abundance was significantly higher in the treatment ($p = 0.047$), while density (SDI) was marginally higher relative to the control (Table 1). For non-whitebark pine trees, we found significantly fewer trees ($p = 0.002$), lower basal area ($p < 0.001$), and lower density (SDI; $p < 0.001$) in the treatment (Table 1).

Blister rust was relatively low in 2014, with only 8 of the 91 sampled trees (~9%) showing symptoms. However, blister rust had increased by the 2023 sampling period, where we documented 16% incidence in the control (symptoms on 10 out of 62 live whitebark pine trees) and 29% incidence in the treatment (symptoms on 34 out of 116 live whitebark pine trees; Table 1). Mortality among whitebark pine trees was similar across both the control (26%) and treatment (25%), while mortality for non-whitebark pine trees was significantly lower in the control ($p = 0.019$; Table 1) due to the intentional mechanical girdling of non-whitebark trees in the treatment.

Thinning effects on whitebark pine tree growth

Whitebark pine trees sampled across the study units in the 2014 campaign ranged in age from 19 to 279 years, with an average age of 120 years. Of the 91 trees sampled, trees growing in the control were ~34 years older on average than trees growing in the treatment, with the majority of sampled whitebark pine trees across both the treatment and control establishing post-1900 (Appendix S1: Figures S2 and S3). Tree diameter (diameter at the height increment cores were collected) was similar across all trees sampled in 2014 (~13 cm diameter; Appendix S1: Figure S4).

When considering the full time series (1833–2014), whitebark pine trees growing in the control exhibited

TABLE 1 Number of live whitebark pine and non-whitebark pine seedlings (<1.38-m tall), saplings (≥1.2 m tall and <12.7 cm diameter), and trees (>12.7 cm diameter) per hectare in 2023.

	Whitebark pine			Non-whitebark pine			Percentage whitebark pine	
Class or characteristic	**Control**	**Treatment**	***p***	**Control**	**Treatment**	***p***	**Control**	**Treatment**
Seedling height class (m)								
<0.15	2083	4236	0.37	1871	0	**0.011**	53	100
0.15–0.46	424	247	0.604	1906	459	0.189	18	35
0.46–0.76	353	212	0.58	1200	1059	0.217	23	17
0.76–1.07	71	71	*NA*	671	106	0.117	10	40
1.07–1.38	35	106	0.546	671	0	**0.031**	5	100
Sapling dbh Class (cm)								
<2.54	184	85	0.218	904	14	**0.002**	17	86
2.54–5.08	42	92	0.412	551	0	**0.001**	7	100
5.08–7.62	14	42	0.336	254	0	**0.004**	5	100
7.62–10.16	49	42	0.619	106	0	0.075	32	100
10.16–12.7	7	0	0.391	28	7	0.259	20	0
Tree demography								
Density (>12.7 cm)	297	544	**0.047**	406	42	**0.002**	42	93
Basal area (m^2 ha^{-1})	45.4	35	0.535	25.9	1.9	**<0.001**		
SDI (metric)	176	244	0.073	146	14	**<0.001**		
BR occurrence (%)	16	29	0.124	NA	NA	NA		
Mortality (%)	26	25	0.848	17	100	**0.019**		

Note: Reported *p* values are from the nonparametric Wilcoxon rank sum test comparing control and treatment. Values in boldface reflect statistical significance at the $\alpha < 0.05$ level.
Abbreviations: BR, blister rust; NA, not applicable; SDI, stand density index.

marginally greater growth, particularly from 1900 to 2000, compared with trees growing in the treatment (Figure 1A,B). Beginning around the year 2000, whitebark pine trees in both the treatment and control experienced an increased growth trend that persisted through to sampling in 2014. However, relative to trees growing in the control, trees growing in the treatment experienced a much greater release in radial growth (RWI and BAI). Whitebark pine trees growing in the treatment exhibited a 52% increase in RWI ($p < 0.001$) and a 60% increase in BAI ($p < 0.001$; Figure 1C,D). Whitebark pine growing in the treatment experienced ~22 cm^2 of radial growth on average in the nine years following the thinning treatments, compared with ~9 cm^2 of radial growth in the control (Figure 1D).

The small diameter (<5 cm dbh) whitebark pine trees in the treatment dramatically increased in radial growth in the posttreatment time period (2003–2011), with a 74% increase in RWI ($p < 0.001$; Figure 2) and an over 90% increase in BAI ($p < 0.001$). These small trees had ~32 cm^2 of growth on average in the nine years following the thinning treatments compared with ~1.2 cm^2 of average growth in the pretreatment period (1990–1998).

Thinning effects on resin duct morphology

Following the 1999–2002 thinning treatments, whitebark pine trees in the treatment produced 34% more resin ducts on average compared with trees in the control ($p < 0.001$; Figure 3A). In addition, resin ducts were 23% larger ($p < 0.001$) and had 49% increased area ($p < 0.001$) for trees in the treatment (Figure 3B,C), but significantly lower resin duct density (48%; $p = 0.002$; Figure 3D) compared with trees in the control. Overall, differences in radial growth and resin duct morphology collectively explain a significant amount of variance (~85%) in the posttreatment time period across whitebark pine trees (Figure 4).

Factors affecting growth and resin duct relationships

Whitebark pine tree size (diameter at core height) positively correlated with BAI ($r = 0.63$, $p < 0.001$) and negatively correlated with standardized resin duct metrics (duct density; $r = -0.19$, $p = 0.012$ and relative duct area; $r = -0.21$, $p = 0.006$) over the pre- and posttreatment

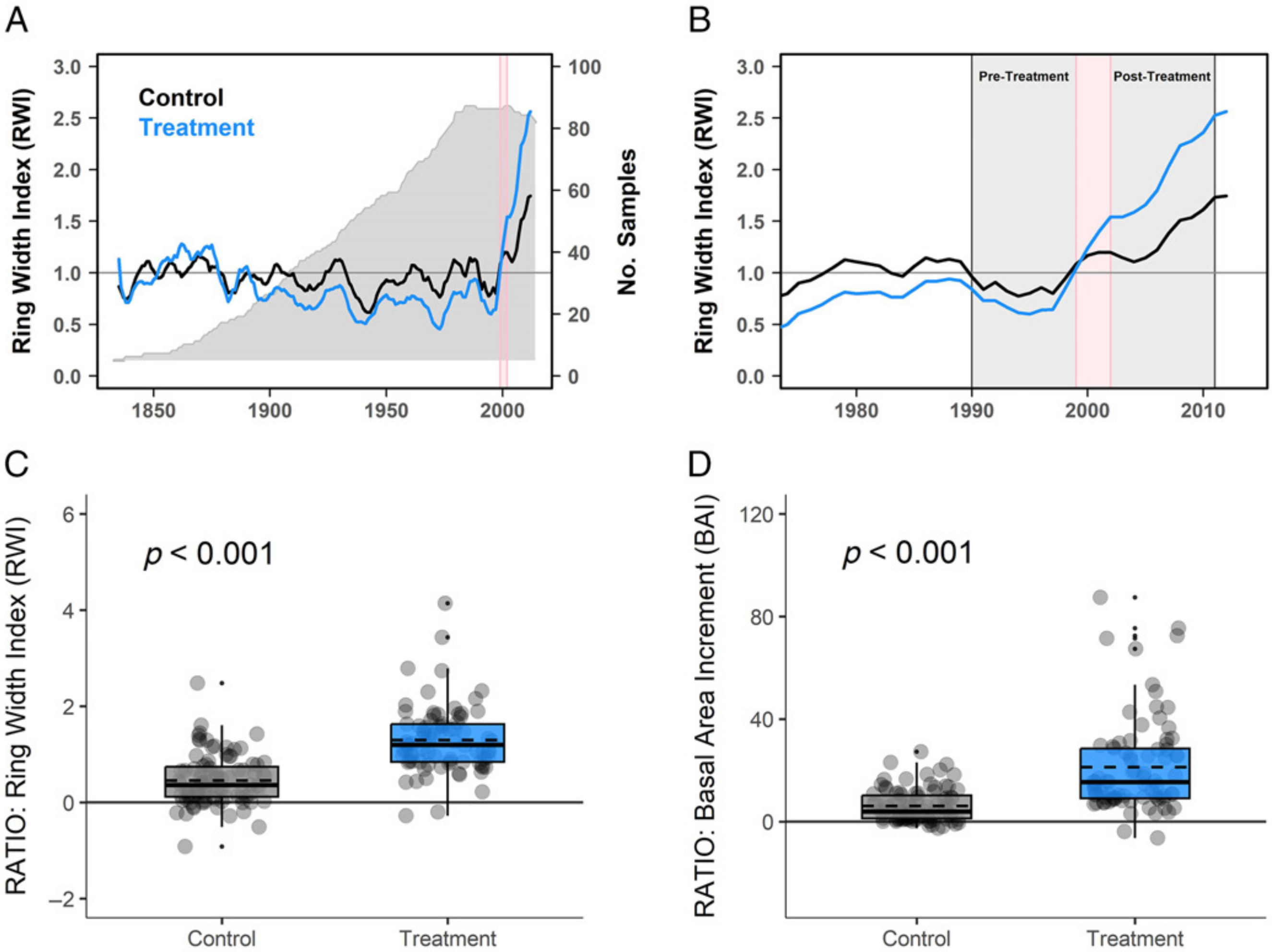

FIGURE 1 (A) Time series of the full ring width index (RWI) series from 1833 to 2014 and sample depth (gray area; right *y*-axis) and (B) a magnified view of the series from 1975 to 2014. The RWI series were developed from 91 whitebark pine trees sampled across the control (black) and treatment (blue). The gray horizontal line represents average growth for the RWI series. The red shading represents the window of thinning treatments (1999–2002) that were excluded from our analyses comparing pre- and posttreatment growth and resin duct morphology, while the gray shading (in B) represents pre- and posttreatment analysis periods, respectively. (C, D) Boxplot comparison of the ratio of (C) tree growth (unitless RWI) and (D) basal area increment (in square centimeters per year; BAI) across the control (black) and treatment (blue). The ratio was calculated as the average difference between the nine years pre-thinning (1990–1998) and nine years post-thinning treatments (2003–2011), where positive values reflect increases in post-thinning years compared with pre-thinning years. Boxplots illustrate median (solid line), mean (dashed line), first and third quartiles (boxes), outliers (small black dots), and range of data (jittered gray dots).

analysis period (1990–2011). For trees in the treatment, tree size was positively related with resin duct size ($r = 0.22$, $p = 0.043$; Table 2). In contrast, tree age for whitebark pine in both the control and treatment negatively correlated with resin duct production ($r = -0.46$, $p < 0.001$), duct size ($r = -0.22$, $p = 0.009$), and duct area ($r = -0.45$, $p < 0.001$), suggesting a decrease in resin duct defenses with increased age (Appendix S1: Figure S5). In the treatment, tree age was positively related with both RWI and BAI ($r = 0.5$, $p < 0.001$; $r = 0.52$, $p < 0.001$, respectively). In the control, resin duct density was positively related to tree age ($r = 0.31$, $p = 0.006$), while relative resin duct area negatively correlated with tree age in the treatment ($r = -0.25$, $p = 0.044$; Table 2). When looking at correlations over the pretreatment (1990–1998) and posttreatment (2003–2011) period separately, we observed similar relationships, although the strength of the relationship between tree growth (RWI and BAI) and tree age declined in the posttreatment period when considering all whitebark pine trees across both the treatment and control (Appendix S1: Table S1).

We did not detect any notable differences in the ratio of growth and resin duct metrics following the thinning treatments due to growth form (e.g., trees growing

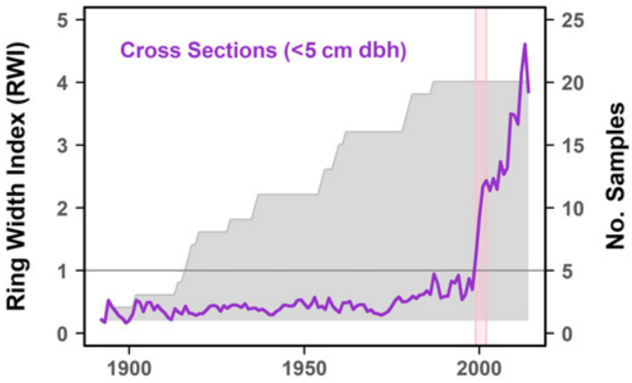

FIGURE 2 Time series of tree growth (ring width index; RWI) from 1892 to 2014 and sample depth (gray area; right *y*-axis) for 20 small diameter (<5 cm dbh) whitebark pine trees sampled in the treatment. The gray horizontal line represents average growth for the RWI series. The red shading represents the window of thinning treatments (1999–2002) that were excluded from our analyses comparing pre- and posttreatment growth.

isolated versus in clumps/groups) (Appendix S1: Figure S6). We also did not detect any significant relationships between stand density (SDI) and whitebark pine physiology over the pre- and posttreatment period (1990–2011; Appendix S1: Table S2). However, for the pairs of blister rust diseased/disease-free whitebark pine trees, we found that over the pre- and posttreatment time period (1990–2011) resin duct production and resin duct area were both greater in diseased trees (32% greater duct production: $p = 0.041$ and 33% greater duct area: $p = 0.035$, respectively; Appendix S1: Figure S7).

In relation to climate, we found that whitebark pine tree growth across both the control and treatment responded positively to warm season (May–September) average temperature (Control, $r = 0.4$, $p < 0.001$; Treatment, $r = 0.4$, $p < 0.001$; Figure 5; Appendix S1: Figure S8). While trees over both the treatment and control had a similar response to temperature, trees in the treated areas experienced a greater increase in radial growth with increased average temperature in the nine years after treatment (Figure 5). In contrast, tree growth across both the treatment and control negatively correlated with precipitation, particularly during the cool season (October of the previous year through April; Control, $r = -0.27$, $p = 0.003$; Treatment, $r = -0.16$, $p = 0.086$; Appendix S1: Figure S8). When looking at climate relationships over the pre- and posttreatment periods separately, we found that the strength of relationships between tree growth (RWI), temperature, and precipitation generally declined in the posttreatment period across both the treatment and control (Figure 5), outside of an increased positive relationship between September minimum temperature and tree growth for both the treatment ($r = 0.69$, $p = 0.014$) and control ($r = 0.72$, $p = 0.009$) and an increased negative relationship between May precipitation and tree growth in the control only ($r = -0.58$, $p = 0.047$; Appendix S1: Table S3). We also observed a general shift in correlations for maximum temperature in the posttreatment period (from positive to negative) in both the control and treatment, particularly for annual average and warm season maximum temperature (Appendix S1: Table S3).

DISCUSSION

Thinning whitebark pine stands to reduce competition of shade-tolerant conifers significantly increased the growth and resin duct defense characteristics of whitebark pine trees across the study area (Figures 1–3). In some instances, the release in both tree growth and resin duct defenses was dramatic (Appendix S1: Figures S9 and S10), as was evident from the increase more than two folds in BAI in treated trees (~22 cm^2 on average posttreatment) relative to those growing in the control (~9 cm^2 on average posttreatment; Figure 3). For the small diameter (<5 cm dbh) trees sampled in the treatment, the growth release was even more significant, with a 74% increase in RWI and ~32 cm^2 average growth in the nine years following the thinning treatment (Figure 2; Appendix S1: Figure S10). We speculate that the reduction in competition of predominately subalpine fir following thinning, improved access to resources conducive to the production of primary and secondary metabolites (e.g., soil nutrients and better availability of sunlight facilitating photosynthesis and carbohydrate production). In addition, ours is the first study to show that thinning positively affected resin duct defenses in whitebark pine. This is an important finding, as the production of more and larger resin ducts with increased duct area translates to an improved capacity to produce, store, and mobilize oleoresin, which is the primary defense of whitebark pine to bark beetles (Hood & Sala, 2015; Kichas et al., 2020, 2021). Additionally, though trees in the smallest size class (<5 cm dbh) are typically too small to produce cones, the significant growth release in these individuals following the thinning treatments provides evidence for maintaining small diameter trees in treatment prescriptions, where possible.

The observed increase in both growth and resin duct defenses is in support of our hypothesis and endorses the use of thinning as an effective management tool within whitebark pine forests in the GYE. While we did detect a significant growth and resin duct release in treated whitebark pine trees, the relatively short time periods used for our analyses (nine years pre- and posttreatments) likely fails to fully capture the duration and magnitude of growth release and change in resin duct morphology for this

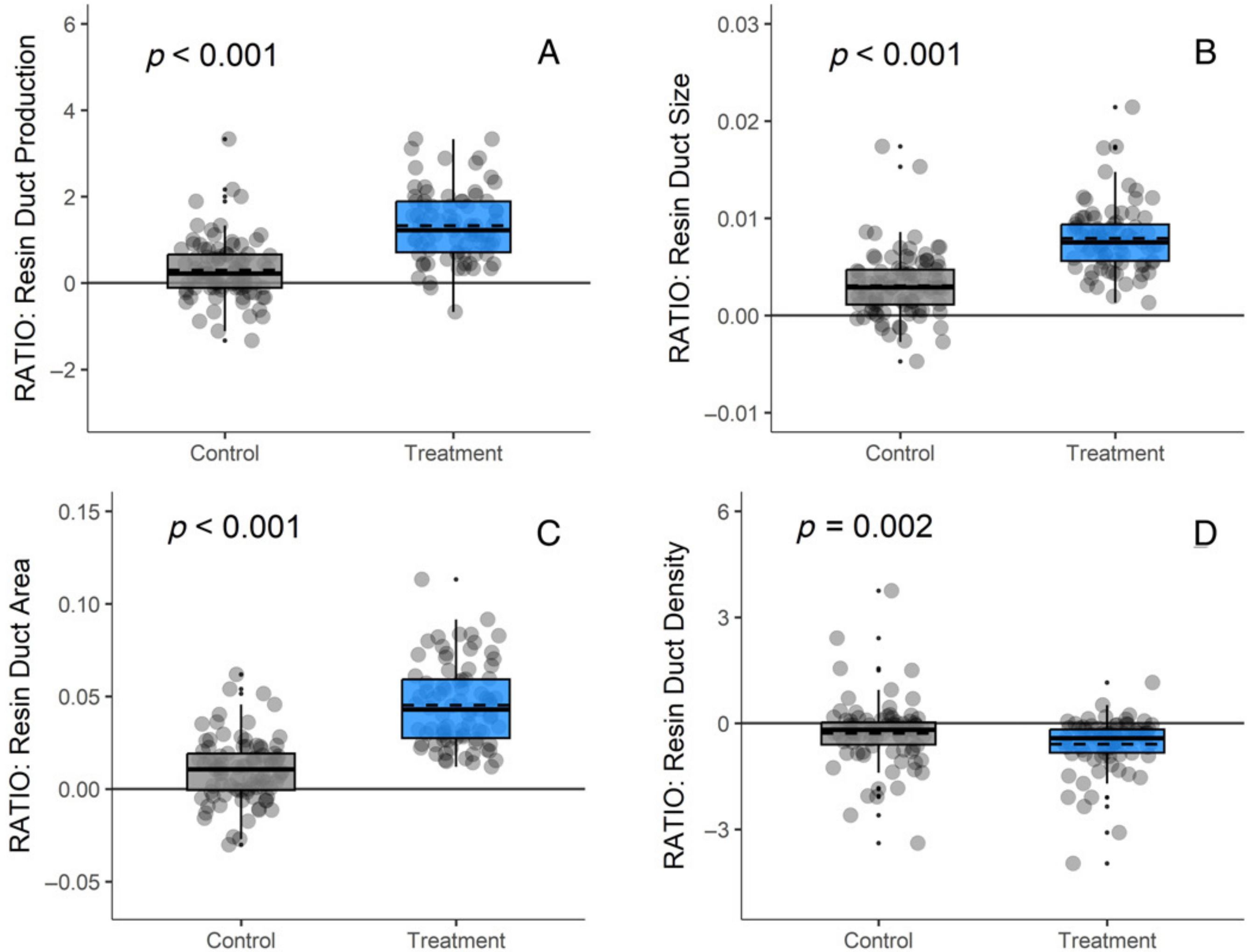

FIGURE 3 Boxplot comparisons of the ratio of (A) resin duct production (number of ducts per year), (B) resin duct size (mean size of all resin ducts per annual ring; in square millimeters), (C) resin duct area (sum of resin duct size: in square millimeters per year), and (D) resin duct density (number of resin ducts per square millimeters per year) across the control and treatment. The ratio was calculated as the average difference between the nine years pre-thinning (1990–1998) and nine years post-thinning treatments (2003–2011), where positive values reflect increases in post-thinning years compared with pre-thinning years. Boxplots illustrate median (solid line), mean (dashed line), first and third quartiles (boxes), outliers (small black dots), and range of data (jittered gray dots).

long-lived species. An important caveat to these observations is that our tree-ring data were collected from live individual trees and do not capture stand-level mortality and growth patterns. The relative abundance of whitebark pine seedling and saplings can vary, depending on the different forest types where whitebark pine occurs (Goeking et al., 2018; Goeking & Izlar, 2018). Based on our 2023 surveys, while both the control and treatment had notable levels of whitebark pine seedlings, saplings, and trees (Table 1), we observed striking differences in the relative abundance of whitebark pine. Relative dominance of whitebark pine was much higher in the treatment compared with the control for all size classes (77% whitebark pine in the treatment versus 29% whitebark pine in the control; Table 1). Regeneration in the control was heavily dominated by subalpine fir and Engelmann spruce; therefore, competition with these shade-tolerant conifers will likely inhibit whitebark pine seedling and sapling growth and future establishment of cone-bearing trees. Removal of competing conifers in the treatment created conditions favorable to whitebark pine seed caching by Clark's nutcracker and seedling establishment while promoting enhanced growth and defense of preexisting saplings and trees. We also found that whitebark pine tree mortality was similar across both the control (26% mortality) and the treatment (25% mortality), indicating that the thinning treatments did not have any adverse impacts on tree mortality. The positive effects of thinning on whitebark pine establishment and tree growth, coupled with the lack of elevated mortality in the treatment relative to the control,

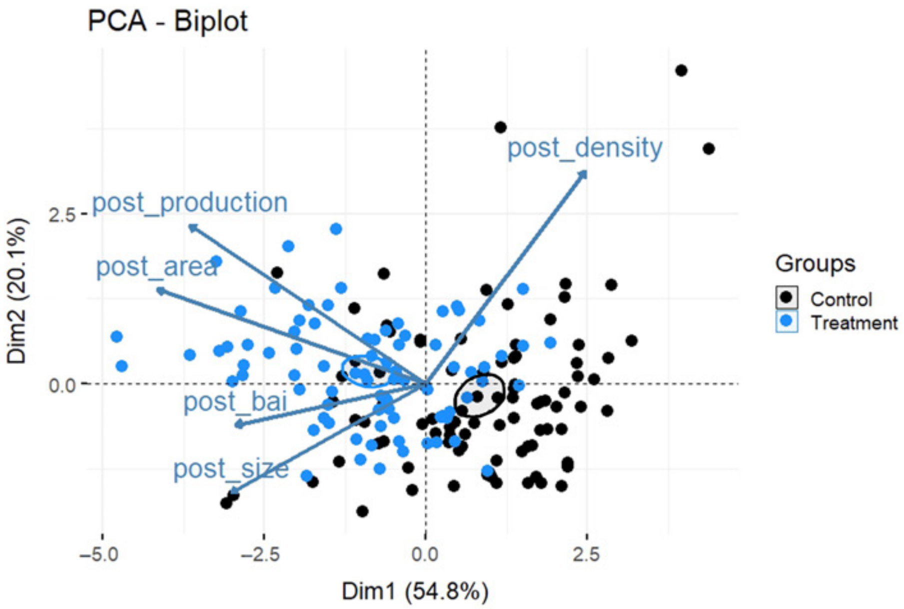

FIGURE 4 Principal components analysis comparing growth (basal area increment; BAI) and resin duct characteristics (duct production, size, area, and density) for 91 live whitebark pine trees post-thinning treatments (period of analysis: 2003–2011). Ellipses are 95th percentile CIs for each grouping. Arrows illustrate the relative contribution of growth and defense metrics to the ordination.

TABLE 2 Spearman correlation coefficients of whitebark pine tree size, tree age, tree-ring growth, and resin duct anatomical measurements.

Characteristic	RW	RWI	BAI	Production	Size	Area	Density	Rel area
Control								
Diameter	0.13	−0.08	**0.52**	0.18	−0.03	0.09	<0.01	−0.04
Age	**−0.43**	−0.11	−0.13	**−0.29**	**−0.29**	**−0.35**	**0.31**	0.17
Treatment								
Diameter	**0.25**	0.21	**0.88**	−0.1	**0.22**	0.04	**−0.44**	**−0.42**
Age	−0.11	**0.5**	**0.52**	**−0.4**	−0.03	**−0.31**	−0.24	**−0.25**
All whitebark pine trees								
Diameter	0.12	0.03	**0.63**	−0.02	0.08	0.03	**−0.19**	**−0.21**
Age	**−0.45**	−0.01	0.03	**−0.46**	**−0.22**	**−0.45**	0.12	0.05

Note: Correlations were conducted on metrics averaged over the pre- and posttreatment period (1990–2011). Values in boldface indicate statistical significance at the $\alpha < 0.05$ level. Age, total age of trees from outermost rings to pith establishment (in years); RW, ring widths (in millimeters); RWI, ring width index; BAI, basal area increment (in square centimeters per year); production, resin duct production (in number of ducts per year); size, resin duct size (in square millimeters); area, duct area (in square millimeters per year); density, resin duct density (in number of ducts per square millimeter per year); rel area, relative resin duct area (% annual ring).

provide strong evidence in support of thinning as a viable silvicultural technique in whitebark pine conservation efforts.

We observed an increase in blister rust between 2014 and 2023, with 13% greater blister rust occurrence in the treated unit, relative to the control (Table 1). It is possible that reduced stand densities, particularly for non-whitebark pine trees, within the thinned unit could amplify airborne transmission of the blister rust pathogen and/or facilitate regeneration of understory *Ribes* spp., potentially negating the seemingly positive benefits of increased growth and resin duct defenses over time. As our study did not investigate these factors directly, ongoing monitoring and observational analyses will be necessary in many whitebark pine stands to better track and understand these patterns and how they may influence the overall success of restoration treatments going forward.

The broader study region experienced mountain pine beetle-caused mortality in lodgepole and whitebark pines between 2006 and 2011 (USDA Forest Service Forest Health Protection, 2024). As our sampled trees were

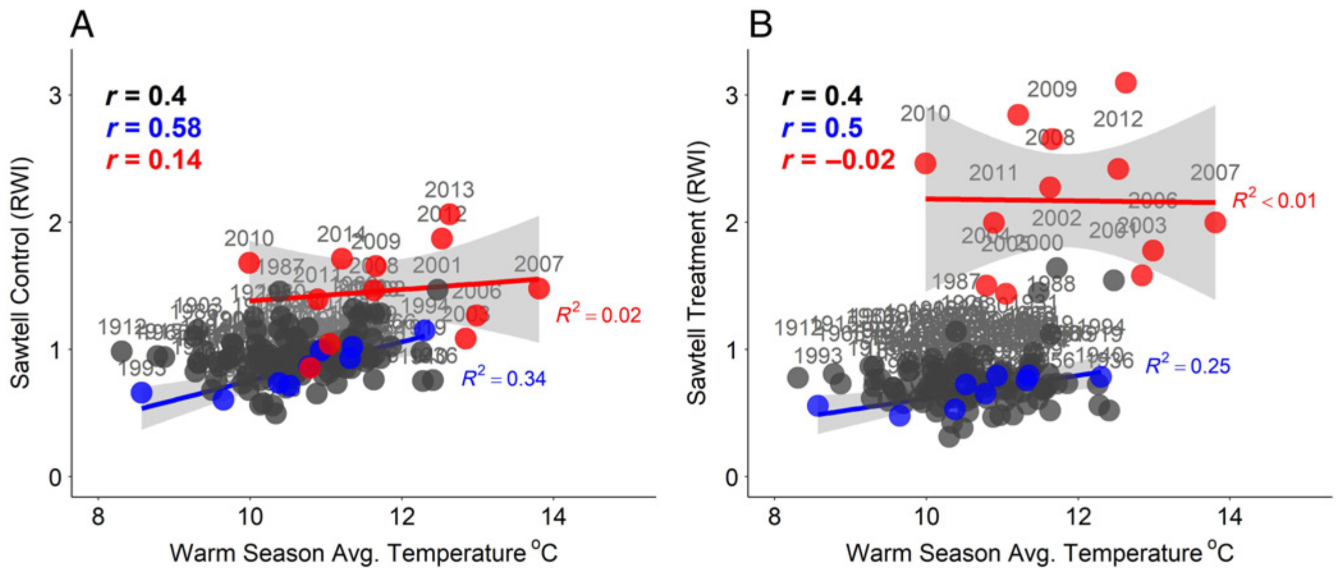

FIGURE 5 Scatterplot relationships of tree growth (ring width index; RWI) and warm season (May–September) average temperature (in degrees Celsius) for whitebark pine trees growing in the (A) control and (B) treatment areas. Blue points represent the pretreatment analysis period (1990–1998), red points represent years posttreatment (2003–2014), and gray points represent all years prior to 1990. Lines represent simple linear regression models with 95% CIs (gray shading) fit to the pretreatment (blue) and posttreatment period (red). Reported correlation coefficients (*r*) are for tree growth (RWI) and warm season average temperature across the full climate record (1895–2014; black), pretreatment period (blue), and posttreatment period (red). R^2 values are reported for the linear models fit for the pretreatment (blue) and posttreatment (red) periods.

mostly too small to be host to mountain pine beetle and verbenone was applied 2010–2012, we are not able to test if the observed increase in resin duct defenses and growth translated to increased survival during the MPB outbreak. However, our 2023 sampling suggests that the thinning did not reduce overstory (>12.7 cm dbh) whitebark pine mortality during the outbreak (Table 1). The outbreak began within about five years of the treatment, and it is possible that trees in the study area did not have time to fully ramp up growth and defenses. Additionally, this epidemic outbreak may have overwhelmed the small treatment area with beetle populations high enough to overcome defenses of even the most resistant trees. Lastly, we do not have data on forest plots prior to 2023, and therefore, our 2023 assessment of forest conditions is relatively small and not the main focus of the study. With this deficit of earlier baseline information, we may not have a sufficient number of plots to fully describe forest conditions over the lifetime of the study. Further research is needed comparing tree growth, resin ducts, and mortality patterns of all tree size classes in thinned and un-thinned areas challenged by bark beetle outbreaks to fully test the efficacy of thinning treatments in whitebark pine ecosystems.

Interestingly, we found positive relationships with tree age and tree growth (RWI and BAI) in whitebark pine trees in both the treatment and control but negative relationships between resin duct production, duct size, and duct area with increasing age (Table 2; Appendix S1: Figure S5). While we did detect a positive relationship with resin duct density and tree age in the posttreatment period, this was driven primarily by trees in the control and was attributable to older trees in the control exhibiting narrower ring widths, resulting in a higher relative frequency of resin ducts per annual ring (Table 2; Appendix S1: Table S1, Figure S5). Whereas trees in the treatment produced more and larger resin ducts posttreatment, ring widths were also significantly greater in older trees (due to the observed growth release post-thinning), resulting in a weaker relationship between duct density (which is standardized to tree growth) and tree age (Table 2; Appendix S1: Table S1, Figure S5). The negative relationship between tree age and unstandardized resin duct metrics for trees in both the treatment and control suggests that, despite experiencing enhanced growth with increasing age, resin duct morphology generally declines in older trees, potentially translating to a reduced capacity for defense against bark beetles (Kichas et al., 2020). While several theories for growth-defense trade-offs have been posited, the growth-differentiation balance hypothesis suggests that defenses are increased under conditions of moderate stress (e.g., nutrient limitation), while both growth and defenses are limited under extreme stress (e.g., moderate-to-severe drought) (Ferrenberg et al., 2015, 2023; Moreira et al., 2015; Stamp, 2003). It is possible that our observations of increased growth but decreased resin duct production, duct size, and duct area for older individuals is reflective of this continuum, whereby adequate resource availability across the study sites (due to relatively abundant moisture and biologically available water) has facilitated increased growth with reduced differentiation of resin duct defenses for older, mature trees sampled for our analyses.

Research has found increased mortality in larger whitebark pine relative to smaller trees in natural, unmanaged stands throughout whitebark pines native range due to mountain pine beetles (Goeking & Izlar, 2018; Simard et al., 2012). Bark beetle-caused mortality in larger trees is more likely under outbreak scenarios, whereas mortality rates are typically higher in smaller-diameter host trees under endemic beetle pressure (Boone et al., 2011; Shanahan et al., 2016). This is, in part, because during outbreak conditions the sheer abundance of beetles can readily overwhelm defenses of even the most vigorous trees. However, tree size and tree age are often uncoupled, especially for slow-growing, long-lived species (Dietrich & Anand, 2019; Piovesan & Biondi, 2020). For example, the largest trees we sampled were 25 cm, yet many were over 150 years old (Appendix S1: Figure S5). The observed overall increase in tree growth, resin duct production, duct size, and duct area in the treatment reflects improved vigor and an enhanced capacity to defend against bark beetles, which may offset future beetle-related mortality as these trees grow to preferred host size. Although, of note, resin duct characteristics and resin-based defenses are under genetic control (Moreira et al., 2015; Westbrook et al., 2015) and, as such, may not respond uniformly across diverse biogeographic gradients. In addition, resin chemistry and the composition of oleoresin are critical factors influencing bark beetle interactions (Raffa, 2014; Raffa et al., 2005; Smith, 2000). Research has demonstrated that resin duct anatomy and resin chemistry are decoupled, thus presenting beetles with many permutations of anatomical and chemical resin-based defenses (Kichas et al., 2021; Mason et al., 2019; Raffa et al., 2017). Further, constitutive resin ducts and resin chemistry are but one aspect of defense to bark beetles and their fungal symbionts, while induced defenses (e.g., formation of traumatic resin ducts and changes in xylem and phloem resin chemistry upon exposure to beetles and pathogens) are equally important components of tree defense (Howe et al., 2020). While our study did not consider induced defenses, our findings highlight the complexities in understanding the nuanced relationships of tree growth and defense and warrant additional research examining resin duct characteristics in whitebark pine at landscape to regional scales, as well as in pre- and post-outbreak scenarios, where applicable.

It is also important to consider vulnerability to mountain pine beetle in context with life history requirements of whitebark pine. Whitebark pine is moderately shade intolerant and is outcompeted by more shade-tolerant species such as Engelmann spruce and subalpine fire (Arno & Hoff, 1989; Tomback et al., 2022). While whitebark pine can persist in the understory and midstory for many decades, these smaller statured trees will not produce cones. Also, whitebark pine infected with blister rust reduces cone production and seed viability through increased mortality of cone-bearing branches and observed increases in seed predation in stands with high blister rust occurrence (Maloney et al., 2012; McKinney & Tomback, 2007; Tomback et al., 2022). Therefore, it is important to develop management strategies that can enhance growth rates while not increasing blister rust infection to improve the likelihood of recruiting whitebark pines into the overstory that will more likely produce cones for improving genetic diversity of the species. Planting seedlings and breeding individuals for rust resistance are effective tools in restoration treatments, coupled with preserving genetic variability within naturally occurring whitebark pine stands since surviving trees have demonstrated a capacity to respond to changes in biotic and abiotic pressures over time (Kichas et al., 2020, 2023). Silvicultural thinning is an effective strategy in this regard as the genetic component of whitebark pine is preserved on landscapes where whitebark pine populations have naturally established.

We did not detect any significant difference in growth and resin duct metrics for whitebark pine trees growing in solo versus clumped formation (Appendix S1: Figure S6). This may be useful for managers as it suggests that the observed growth and defense benefits from thinning activities are not readily influenced by growth form, and thus, efforts to retain whitebark pine populations using restoration treatments have added flexibility in evaluating optimal trees for treatment. In addition, we found some evidence for increased resin duct production and increased duct area for whitebark pine trees with blister rust, which suggests that diseased trees are responding to the pathogen with increased resin-based defenses (Appendix S1: Figure S7). While resin exudation is a commonly observed symptom of blister rust infection in whitebark and other five-needle pines, research quantifying resin duct anatomy and blister rust susceptibility is limited. Indeed, we are aware of only one other study that has examined these relationships in conifers. Holtz and Schoettle (2018) found no difference in resin duct characteristics between blister rust resistant and nonresistant limber pine, which is physiologically similar to whitebark pine. While we did observe increased duct production and duct area with blister rust occurrence in whitebark pine, our sample size is small, and our study was not specifically designed to test for these interactions. Given the importance of resin duct anatomy as a primary defense against bark beetles and potential synergies of bark beetles and blister rust contributing to tree mortality (Bockino & Tinker, 2012; Holtz & Schoettle, 2018; Six & Adams, 2007), future studies should consider the extent to which blister rust influences resin duct morphology and if and how resin duct properties differ between blister rust susceptible and blister rust resistant trees. This is especially important as planting of rust-resistant seedlings has been recognized as a major initiative in whitebark pine restoration (Tomback et al., 2022) and, to our knowledge, many breeding programs do not assess resin duct characteristics and resin-based defenses as part of this process.

The observed increase in whitebark pine tree growth in both the treatment and control beginning around the year 2000 (Figure 1), coupled with the positive response of tree growth to warm season temperature (Figure 5; Appendix S1: Figure S8) suggests that these trees are responding favorably to enhanced growing season conditions in these high-elevation environments. Whereas the negative relationships between tree growth and precipitation, particularly during the cool season, is likely attributable to the establishment and persistence of snowpack and increased cloud cover in winter months, limiting photosynthesis and xylogenesis. Similar increases in tree growth in high-elevation bristlecone pine trees beginning in the latter part of the 20th century have been observed across both California and Nevada (Bunn et al., 2018; Salzer et al., 2009), while Dudney et al. (2023) and van Mantgem et al. (2023) also reported similar increases in whitebark pine tree growth in high-elevation, energy-limited Sierra Nevada populations corresponding with warmer temperatures. These findings are further supported by Kichas et al. (2023), who found similar temperature-driven increases in whitebark pine tree growth and resin duct morphology in northwestern Montana, indicating that these are energy-limited rather than moisture-limited ecosystems. Collectively, these observations suggest that at least some subalpine environments in the Western United States are responding positively to anthropogenic warming, particularly over the last 150 years, which has likely facilitated earlier snowmelt and extended growing season conditions in these high-elevation environments, resulting in increased photosynthesis, carbon sequestration, and tissue formation (ring growth) in historically temperature-limited ecosystems. The positive growth response of whitebark pine to regional warming and extended growing season conditions could greatly benefit management activities aimed at enhancing whitebark pine vigor, as trees are naturally responding to climatic conditions favorable for growth and establishment. As noted by Kichas et al. (2023), this trend is unlikely to continue indefinitely, and at some point (possibly within the next several decades), these high-elevation, energy-limited environments will eventually transition to water-limited systems with ongoing warming and thus be more susceptible to drought stress and associated mortality (Dudney et al., 2023). Of note, we observed a general weakening of the relationship between tree growth and warm season average temperature in the posttreatment time period (Figure 5), as well as a shift in correlations between tree growth and maximum temperature in the posttreatment period (from positive to negative; Appendix S1: Table S3). Although these relationships were not statistically significant, they could reflect an upper threshold under which tree growth is negatively impacted under the highest temperatures in the most recent years of our climate record. However, the time period of our posttreatment analysis is relatively short (2003–2014) and as such may not accurately capture the more nuanced aspects of multiyear tree growth to interannual climate variability. In addition, warming temperatures, particularly in fall and winter can promote increased mountain pine beetle activity (Buotte et al., 2016, 2017; Robbins et al., 2022), which may negate the seemingly potential benefits of enhanced tree growth and resin duct morphology. On the other hand, resin viscosity is also influenced by air temperature and can more readily mobilize in warmer versus colder environments (Perrakis & Agee, 2006; Smith, 2000), although, warmer and more humid conditions can also increase the likelihood of infection by blister rust (Thoma et al., 2019). Given these factors, more research is needed to better understand how management treatments, coupled with changing climate and disturbance pressures, influence whitebark pine growth and resin duct anatomy over longer time periods.

CONCLUSIONS

We found that whitebark pine trees (>12.7 cm dbh) in our study responded favorably to thinning and experienced a 60% increase in BAI (52% increase in RWI), while also producing 34% more resin ducts that were 23% larger with 49% increased area in the nine years post-thinning compared with trees in the control. Thinning also created conditions favorable for whitebark pine seedling and sapling establishment, whereby 75% of seedlings and 93% of saplings in the treatment were whitebark pine, compared with 32% seedlings and 14% saplings in the control. Moreover, the absence of increased mortality in the treated areas strongly supports thinning as a sustainable silvicultural practice for whitebark pine conservation efforts. Our findings support reducing conifer competition in whitebark pine forests where feasible to improve growth, resin duct defenses, and regeneration. Additional research on the effects of various treatments across a range of diverse environments and ongoing monitoring of the response of whitebark pine to such treatments over time is needed.

AUTHOR CONTRIBUTIONS

Nickolas E. Kichas contributed to formal analysis, investigation, methodology, data curation, writing—original draft, and writing—review and editing. Erin K. Shanahan contributed to conceptualization, methodology, investigation, resources, data curation, writing—review and editing, and funding acquisition. Sharon M. Hood contributed to conceptualization, methodology, investigation, resources, supervision, project administration, and funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kichas et al., 2024a, 2024b) are available from the National Centers for Environmental Information: https://doi.org/10.25921/fmfg-b579 (ring width data) and https://doi.org/10.25921/fnds-7640 (resin duct data).

ORCID

Nickolas E. Kichas https://orcid.org/0000-0002-7817-2078
Erin K. Shanahan https://orcid.org/0000-0002-5279-9825
Sharon M. Hood https://orcid.org/0000-0002-9544-8208

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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