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Growth and defense characteristics of whitebark pine (*Pinus albicaulis*) and lodgepole pine (*Pinus contorta* var *latifolia*) in a high-elevation, disturbance-prone mixed-conifer forest in northwestern Montana, USA

Nickolas E. Kichas [a,*], Amy M. Trowbridge [b], Kenneth F. Raffa [b], Shealyn C. Malone [b], Sharon M. Hood [c], Richard G. Everett [d], David B. McWethy [e], Gregory T. Pederson [f]

[a] Montana State University, Bozeman, MT, United States
[b] University of Wisconsin, Madison, WI, United States
[c] U. S. Forest Service, Rocky Mountain Research Station, Missoula, MT, United States
[d] Salish Kootenai College, Pablo, MT, United States
[e] Montana State University, Bozeman, MT, United States
[f] U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT, United States

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ABSTRACT

Recent, widespread tree mortality in the western U.S. resulting from changes in climate, pathogens, insect activity, and forest management practices has led to concerns for many ecologically and culturally important species. Within conifers, resin-based defenses have long been recognized as a primary defense mechanism against a variety of insects and pathogens. Oleoresin produced by trees contain complex mixtures of terpenoids that have numerous insecticidal and fungicidal properties. Research has also identified links between resin duct characteristics and increased probability of survival during bark beetle outbreaks. Whitebark pine (*Pinus albicaulis*) is a culturally significant high elevation species that provides numerous ecological services within subalpine and alpine ecosystems. Whitebark pine has co-evolved with a suite of biotic and abiotic disturbances. Individual trees allocate resources towards growth and resin-based defenses, making it a good candidate species to evaluate growth and defense relationships and tradeoffs. In this study we compared constitutive resin chemistry, tree growth and resin duct anatomy between similarly aged whitebark and lodgepole pine (*P. contorta* var *latifolia*) growing in proximity within a disturbance-prone, mixed-conifer forest in northwestern Montana. These two host species have varying degrees of historical exposure to mountain pine beetle. Our research yields four important findings. First, we did not find evidence of a tradeoff between tree growth and tree defenses (resin duct morphology and resin chemistry). This suggests that trees growing under favorable field conditions can experience high growth rates and still allocate ample resources towards defense. Second, we found that resin ducts and constitutive mono- and sesqui- terpenes were not correlated in lodgepole pine while duct production and area were positively related to constitutive monoterpenes, and duct size and area were positively related to constitutive sesquiterpenes, in whitebark pine. The lack of distinct, consistent relationships between these defensive features suggests that both whitebark and lodgepole pine trees present beetles with numerous, complex combinations of resin-based defenses. Third, based on constitutive terpene profiles, bark beetles are more likely to enter lodgepole pine but more likely to successfully elicit mass attacks in whitebark pine, which agrees with beetle attack and success patterns observed in the field. Fourth, overstory competition, particularly by Engelmann spruce (*Picea engelmannii*), can influence tree defenses, specifically by reducing constitutive terpene concentrations in lodgepole and whitebark pine. Competitive tree interactions could lead to altered bark beetle-conifer interactions as host and nonhost species migrate in response to changing climate. Our results suggest that strategies designed to support whitebark pine populations can benefit from better understanding interactions among growth, competition and physical and chemical defenses in response to multiple disturbance.

* Corresponding author.

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1. Introduction

Recent, large-scale tree mortality in the western U.S. resulting from changes in climate, biotic stressors, and forest management practices has led to concerns for many ecologically and culturally important species (Mattson and Haack 1987, van Mantgem et al. 2004, van Mantgem and Stephenson 2007, Schwandt et al. 2010, Tomback and Achuff 2010, Roy et al. 2014). Given the ecological and economic implications of large-scale mortality events, there is growing interest to better understand physiological strategies employed by trees in response to these shifting disturbance regimes. However, identifying general trends is complicated by the inherent complexity associated with tree defense anatomy and chemistry, both of which vary across populations, individuals, and plant organs (Trowbridge 2014, Jamieson et al. 2017). Large inter- and intra-specific variation in tree physiology and fluctuating disturbance regimes complicates our ability to make generalized assumptions (e.g., that tree mortality can be predicted based on a particular suite of physiological attributes), which hinders development of effective management solutions that account for complex species-specific responses to biotic and abiotic processes.

Within conifers, resin-based defenses have long been recognized as a primary defense mechanism against a variety of insects and pathogens (Lewinsohn et al. 1991, Langenheim 1994, Phillips and Croteau 1999, Trapp and Croteau 2001, Franceschi et al. 2005, Keeling and Bohlmann 2006). Oleoresin produced by trees contains complex mixtures of terpenoids (monoterpenes, sesquiterpenes and diterpenes) (Phillips and Croteau 1999) that have numerous insecticidal and fungicidal properties (Langenheim 1994, Raffa 2014, Trowbridge et al. 2016, Celedon and Bohlmann 2019). Many of these compounds (e.g., monoterpenes) have demonstrated linkages to insect behavior and physiology, from facilitating biosynthesis of communicative pheromones and influencing flight orientation and/or host selection to disrupting the production of crucial enzymes linked to insect growth and biological development (Seybold et al. 2006, Borden et al. 2008, Raffa 2014, Celedon and Bohlmann 2019, Jones et al. 2019).

Resinous compounds are produced, stored, and mobilized within a network of resin duct structures that are connected vertically and horizontally throughout the tree, facilitating rapid mobilization of resins to sites of injury or infection (Hood and Sala 2015, Celedon and Bohlmann 2019). Resin ducts are embedded within annual growth rings (secondary xylem tissues), allowing retrospective quantification of tree carbon allocation between growth and constitutive defenses (Kane and Kolb 2010, Ferrenberg et al. 2014, Ferrenberg et al. 2015, Hood and Sala 2015). Several studies have found relationships between resin duct characteristics (e.g., number of ducts produced, duct size, area, density) and increased probability of survival during bark beetle outbreaks (Kane and Kolb 2010, Ferrenberg et al. 2014, Hood et al. 2015, Hood et al. 2016), drought (Gaylord et al. 2007, Gaylord et al. 2013, Gaylord et al. 2015), and wildfire (Hood et al. 2015, Hood et al. 2016, Slack et al. 2016, Sparks et al. 2017).

Resin duct anatomy is highly variable within and across species and it is unclear as to which growth and defense characteristic(s) may influence survival under biotic and abiotic pressures. For instance, larger resin ducts have been reported in ponderosa pine (*Pinus ponderosa*) (Kane and Kolb 2010, Hood et al. 2015) and whitebark pine (*P. albicaulis*) (Kichas et al. 2020) that persisted through beetle activity, while the opposite (smaller resin ducts) was reported in surviving limber pine (*P. flexilis*) (Ferrenberg et al. 2014). Zhao and Erbilgin (2019) reported larger resin ducts for lodgepole pine (*P. contorta* var. *latifolia*) that persisted through a bark beetle outbreak, while Ferrenberg et al. (2014) did not detect any difference in duct size for surviving lodgepole. There are also inconsistencies in the literature regarding other duct metrics. For instance, Kichas et al. (2020) reported greater duct production and duct density in whitebark pine that died during beetle outbreaks while Kane and Kolb (2010) and Ferrenberg et al. (2014) reported greater production and density in surviving ponderosa and limber pine. Tree growth is equally complex, with research demonstrating higher growth in surviving trees relative to trees that died from bark beetle attack (Ferrenberg et al. 2014, Hood et al. 2015), while other research has found the opposite (greater relative growth in trees that died compared to trees that survived) (Ferrenberg et al. 2014, Kichas et al. 2020) or no trend at all (Kane and Kolb 2010). Such nuanced and species-specific responses complicate our understanding of how these defensive features function over diverse biogeographic gradients (Ferrenberg et al. 2014, Hood and Sala 2015, Kane et al. 2017, Kichas et al. 2020).

An important component influencing tree survival in the presence of insect pressure is the chemical composition of the resin itself (Table S1) (Duhl et al. 2013, Raffa 2014, Keefover-Ring et al. 2016). While many species of conifers produce similar chemicals (e.g., α-pinene, limonene, β -myrcene), the relative composition and concentration of these compounds vary considerably across taxa as well as with biological development and local environment (Smith 2000, Moreira et al. 2014, Raffa 2014, Moreira et al. 2015, Moreira et al. 2016). This variability leads to diverse and largely unknown interactions with insects and pathogens that can facilitate significant change in forest composition and structure. For instance, mountain pine beetle (*Dendroctonus ponderosae*) uses the host monoterpene (−)-α-pinene as a precursor to the synthesis of its aggregation pheromone (−)-*trans*-verbenol, (Pitman et al. 1968, Blomquist et al. 2010, Keeling 2016, Chiu et al. 2019) and β -myrcene and δ-3-carene as synergists of flying beetles' attraction to (−)-*trans*-verbenol (Seybold et al. 2006, Borden et al. 2008). However, numerous other terpenes exhibit insecticidal and fungicidal properties. For instance, δ-limonene is highly toxic to insects, and the phenolic phenylpropanoid 4-allylanisole (aka estragole) inhibits attraction to pheromones (Hayes and Strom 1994, Joseph et al. 2001, Hofstetter et al. 2005). Some of these compounds (e.g., α-pinene and β -pinene) also serve as indirect defenses by attracting parasitoids of bark colonizers (Mizell et al. 1984, Erbilgin and Raffa 2001, Seybold et al. 2006). Along with monoterpenes, sesquiterpenes represent a significant component of constitutive oleoresin, yet their ecological role(s) in bark beetle-conifer interactions is unknown. Sesquiterpenes have been shown to be highly active in other, unrelated systems (Prasifka et al. 2015, Zhang et al. 2015, Zhang et al. 2018, Zhao et al. 2020), and they may influence resin viscosity (Keefover-Ring et al. 2016). However, there is currently no research demonstrating the effects of sesquiterpenes on bark beetles or their symbionts. Additionally, terpene diversity (a measure of relative composition and abundance of compounds) may play an important role in beetle-conifer interactions (Reid et al. 2017). A higher diversity of compounds could theoretically provide trees with a greater phytochemical arsenal in dealing with a variety of herbivores and pathogens. However, it is unclear if there are any relationships between terpene diversity, resin duct anatomy, and tree growth.

There are many interacting factors that could readily alter the growth and defense strategies of trees. For instance, fire, drought, insect, and pathogen activity have been found to influence defensive features (resin flow, resin chemistry and resin duct anatomy) in conifers (Perrakis et al. 2011, Powell and Raffa 2011, Gaylord et al. 2015, Hood et al. 2015, Valor et al. 2017). Competition for resources has long been recognized as an important factor mediating both growth and defense in coniferous tree species (Coomes and Grubb 2000, Larocque et al. 2013) and research has demonstrated increased diameter growth of remaining trees in both natural and managed forest stands when near-tree competition is reduced through various silviculture treatments (Keane et al. 2007, Hood et al. 2016, Tepley et al. 2020). Yet, studies quantifying the effects of competition on conifer defenses (duct anatomy and resin chemistry) are surprisingly limited (Ormeno et al. 2007, Slack et al. 2017). Resin-based defenses are costly to manufacture and maintain, and competition constrains cellular differentiation and biosynthesis of secondary metabolites (Herms and Mattson 1992), altering allocation to growth and defenses. In many ecosystems, biotic and abiotic disturbances drive forest structure and composition, creating a patchwork mosaic of diverse species assemblages in various age classes (Baker

2009). Western U.S. forests are prone to wildfire, insect herbivory and pathogens, which can differentially modulate stand development (Boone et al. 2013, de la Mata et al. 2017, Holtz and Schoettle 2018, Howe et al. 2018). Competition within these forest stands likely influences how trees allocate resources between growth and investment in physical and chemical defenses; however, this is an area of research that is poorly explored. Indeed, we are aware of only three studies that have investigated potential relationships between near-tree competition and the anatomical (Slack et al. 2017) and chemical (Raffa and Berryman 1982, Ormeno et al. 2007) components of resin duct defenses.

Whitebark pine is a critical high-elevation species that provides multiple ecological services within subalpine and alpine ecosystems (Logan et al. 2010, Tomback et al. 2016a, Tomback et al. 2016b, Wagner et al. 2018). However, there is growing concern that whitebark pine may be largely extirpated from its current habitat over the next century due to cumulative impacts of climate change, insect-related mortality, changing fire regimes, increased competition from shade-tolerant species, and the invasive exotic pathogen causing white pine blister rust (*Cronartium ribicola*). These stressors, primarily blister rust, have greatly reduced populations, by as much as 90% in some areas of the northern Rocky Mountains (Keane and Arno 1993, Kendall and Keane 2000, Shanahan et al. 2016, Amberson et al. 2018). In December 2020, the U. S. Fish and Wildlife Service formally proposed whitebark pine as a "threatened" species under the Endangered Species Act, which if approved will require careful and adaptive management to sustain and promote remaining populations. Better understanding the physiological responses of whitebark pine to competition and disturbance could provide useful information for resource managers in developing conservation and restoration efforts. Some work has investigated the physical and chemical defenses of whitebark pines in the Greater Yellowstone Ecosystem (Raffa et al. 2013, Raffa et al. 2017, Mason et al. 2019), but this represents only a portion of its overall range, precluding inference to other forest types across a broader range of environments.

Lodgepole pine (*Pinus contorta* var. *latifolia*) is widely distributed throughout western North America and sometimes co-occurs with whitebark pine and other mountain conifers (Lotan and Critchfield 1990). In the Rocky Mountains, lodgepole pine grows in either mixed or pure stands and is fire-adapted. Lodgepole pine has serotinous cones that are held tightly together with resins and are released by heat from fire or persistent hot dry conditions, after which its seeds are distributed by wind (Anderson 2003). Although individual trees can be killed by fire, the prolific release of seed following disturbance provides competitive advantage, resulting in extensive distributions of dense lodgepole pine forests. Lodgepole pine is also the primary host of mountain pine beetle and experiences widespread mortality during outbreaks (Meddens et al. 2012).

We compared growth and resin duct structures between similarly sized lodgepole pine, the most frequent host of mountain pine beetle (Meddens et al. 2012), and whitebark pine, a historically less-exposed host undergoing increased pressure with warming climate (Logan et al. 2010) growing in close proximity within a disturbance-prone, mixed-conifer forest in northwestern Montana. We analyzed tree growth, resin duct morphology, and constitutive phloem chemistry to investigate three questions: 1) **Are there correlations among tree growth, resin duct anatomy, and resin chemistry? 2) How do constitutive resin chemistry and growth vs. defense relationships compare between whitebark and lodgepole pine? 3) Does the abundance and diversity of overstory and understory competition influence resin chemistry for either species?** For question 1, we predicted H_1) trees with greater growth rates and trees producing more numerous and larger resin ducts would have higher concentrations (μg / g of tissue) and diversity of mono- and sesqui- terpenes. We also predicted H_2) trees with greater relative duct area (% annual ring allocated to resin duct structures) would have greater concentrations and diversity of mono- and sesqui- terpenes. For question 2, we hypothesized H_3) whitebark produce a greater abundance of constitutive monoterpenes known to positively influence bark beetle behavior (such as α-pinene, β-myrcene, and δ-3-carene) whereas lodgepole produce a greater abundance of compounds known to influence host-recognition (principally β-phellandrene, which has been found to be a primary compound that mountain pine beetle utilize in its selection of host trees (Huber et al. 2000, Miller and Borden 2000)). We also predicted H_4) lodgepole pine has greater relative growth rates than whitebark pine and produces larger resin ducts with a greater annual investment in resin duct structures (increased relative duct area). We suspect that beetle preference for lodgepole pine has selected for more robust constitutive defenses than whitebark pine and that this combination of increased growth and favorable duct anatomy will correspond with a greater abundance and diversity of mono- and sesqui- terpenes compared to whitebark pine. For question 3, we predicted H_5) increased competition (greater abundance and diversity of neighboring overstory and understory vegetation) results in decreased concentrations and diversity of mono- and sesquiterpenes. We expect that moderately dense, mixed-conifer forest stands of relatively young age comprise a nitrogen-limited system, and as competition increases nutrient availability declines, limiting overall production of primary and secondary metabolites.

2. Methods

2.1. Site description

Data were collected at a high-elevation site on the western slopes of the Mission Range on the Flathead Indian Reservation during the summers of 2016 and 2017 as part of a larger fire-history reconstruction for the Confederated Salish and Kootenai Tribes (CSKT; Fig. 1) (Kichas et al. 2020). The study site is located at approximately latitude: 47.776026, longitude: −113.971389, with an average elevation of 1,916 m. Overstory species include whitebark pine and lodgepole pine, with smaller components of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Understory species consist primarily of grouse whortleberry (*Vaccinium scoparium*), common huckleberry (*V. membranaceum*), dwarf huckleberry (*V. cespitosum*), bear grass (*Xerophyllum tenax*), smooth woodrush (*Luzula hitchcockii*) and menziesia (*Menziesia ferruginea*). Mean annual temperatures at the site are generally cool, with average temperatures ranging from 1° to 6° C with a 20- to 70-day frost-free period. Annual precipitation averages 140 cm, which occurs primarily as snowfall from November to March. Soils are of the Halloway series, consisting of gravelly silt loam and are moderately drained. Lodgepole pine and whitebark pine are codominant at this site, with lodgepole pine comprising 39% of sampled trees (519 of 1320 trees) and whitebark pine representing 36% of surveyed individuals (476 of 1320 trees). The remaining 25% consists of subalpine fir (187 trees; 14%), Engelmann spruce (126 trees; 10%), western larch (*Larix occidentalis*; 9 trees; <1%) and Douglas-fir (*Pseudotsuga menziesii*; 4 trees; <1%). Mortality is also prevalent, with approximately 86% of whitebark trees and 45% of lodgepole pine trees sampled for the fire history study being dead with evidence of bark beetle activity (such as blue staining in retrieved increment cores and/or bark beetle galleries on the bole of sampled individuals). Evidence of disturbance legacies, including wildfires and insect / pathogen outbreaks are common across the sample plots. The broader region has a recent history of documented bark beetle activity in the 1930s, 1960s–1980s and 2002–2009 (Arno and Hoff 1989, Kipfmueller and Swetnam 2002, Buotte et al. 2017, van de Gevel et al. 2017). This portion of the Mission Range is also characterized by mixed- and lethal-severity fire regimes, resulting in a complex mosaic of establishment (CSKT 2000, 2007). White pine blister rust is evident, having been introduced to this region of the Rocky Mountains circa 1950 (Samman et al. 2003, Geils et al. 2010).

2.2. Field sampling

As part of the CSKT fire-history reconstruction project, a 200 m grid

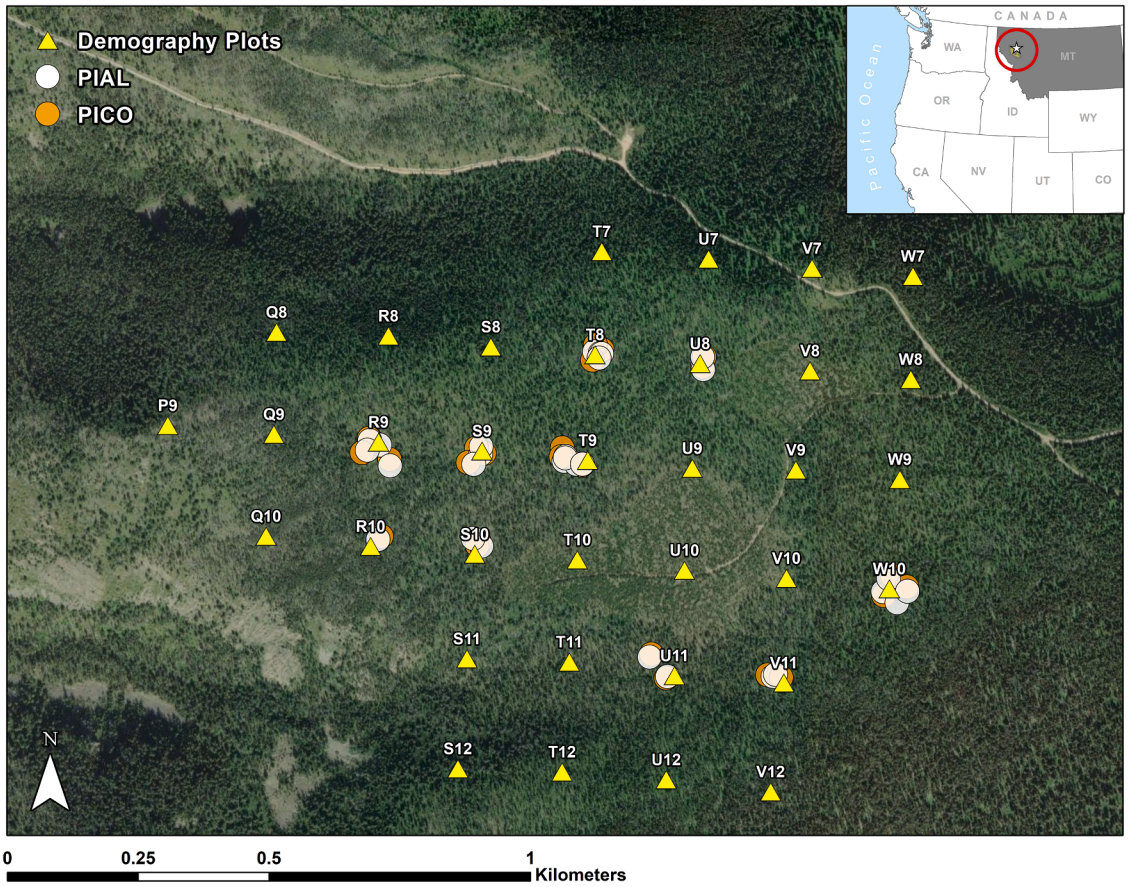

Fig. 1. Map of sampled trees: 30 whitebark pine (white) and 30 lodgepole pine (orange) from a high elevation, mixed-conifer stand in the Mission Range (~4.5 km east of Flathead Lake) on the Flathead Indian Reservation in northwestern Montana. Yellow triangles indicate permanent demography plots that were established in 2016 as part of a larger fire-history study for the Confederated Salish and Kootenai Tribes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was overlain across the study area using a combination of remote sensing and field surveying for optimal placement (Fig. 1). This gridded sampling design captured much of the topographic and vegetative variability across the site, providing for an accurate assessment of disturbance legacies and microsite differences in forest structure and stand composition. Within the 200 m grid, individual plots (hereafter "macroplots") were located 200 m apart with a total of 34 plots, covering approximately 88 ha (Fig. 1).

Each macroplot was spatially referenced and plot centers were permanently marked and tagged. From the macroplot center, four 10 m wide, 100 m long belt transects were established in each cardinal direction (north, south, east, and west; Fig. S1). The closest ten trees within each 100 m transect were sampled (to a maximum distance of 100 m) with a diameter threshold of 15 cm diameter at breast height (DBH) (Heyerdahl et al., 2014). Data collected for each tree at each macroplot included species, condition (live or dead), DBH, canopy base height, crown class (dominant, codominant, intermediate, or suppressed), tree height, and evidence of fire. We collected increment cores from 40 sample trees per macroplot near the base of each tree (at or below 15 cm from the root collar) using Haglöf 4.3 mm diameter increment borers. A 25 m^2 circular microplot was also established around plot center to estimate percent cover of understory species (Fig. S1).

2.3. Field sampling – Terpene composition

From the larger sample of stand-level demographic data, we identified 30 pairs of live whitebark and lodgepole pines for this analysis. To control for microsite variability and visible differences in ontogeny we paired trees based on size (±3 cm DBH) and distance (<15 m apart). In June 2018, individual trees were relocated in the field, across the previously established macroplots. To assess the potential influence of overstory competition on constitutive resin chemistry, we recorded additional information, including species and DBH for all live and dead trees (≥1 cm DBH) within five meters of each subject and for all trees (≥5 cm DBH) to a distance of ten meters (Fig. S2). For understory competition, we identified species and estimated percent cover within a 5.6 m diameter microplot around each subject tree. We collected phloem tissue of approximately 1.5 cm width and 5 cm length for all 60 individuals. Tissue samples were immediately placed in glass vials on dry ice and were transported to Montana State University for storage in a –80° C freezer within 24 h of collection. After the phloem tissues were collected, we retrieved one additional increment core at DBH using 4.3 mm diameter borers within approximately 5 cm from the phloem sampling location.

2.4. Increment core analysis

Increment cores were air-dried and processed using standard dendrochronological techniques (Stokes and Smiley 1996). We measured ring widths to the nearest 0.001 mm using a Velmex measuring stage interfaced with the recording software Measure J2X (Voortech Consulting 2005). We crossdated tree ring series visually and graphically using ring-width patterns and frost rings (LaMarche and Hirschboeck 1984). Crossdating was facilitated using site-specific chronologies from ring-width measurements, which were compiled as

part of a previous study (Kichas et al. 2020) and statistically checked using COFECHA (Holmes et al. 1986, Grissino-Mayer 2001).

Individual tree cores were scanned at high resolution (1200 d.p.i.) on an Epson V550 flatbed scanner and resin duct features were measured 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 defense metrics we followed the methods outlined by Hood and Sala (2015) and collected five measurements, including three non-standardized measures of resin duct size (mean size of all resin ducts per annual ring; mm^2), duct production (number of ducts $year^{-1}$), and total duct area (sum of resin duct size: mm^2 $year^{-1}$), and two measures standardized to tree growth, duct density (number of resin ducts mm^{-2} $year^{-1}$) and relative duct area (% annual ring).

2.5. Analysis of monoterpenes and sesquiterpenes

Following the methods of Trowbridge et al. (2019), phloem tissues were finely chopped (exact weights between ~ 0.2 and 0.3 g) and placed into 2-mL glass vials along with 1 mL of GC-grade n-hexane (Fisher Scientific) containing 0.1 μL mL-1 (+)-fenchone (Sigma-Aldrich) as an internal standard. Samples were then agitated for 24 h, after which 100 μL of the solution from each sample was transferred into micro-inserts in small mouth clear GC vials and capped with PTFE liners (Alltech Associates, Deerfield, IL). Chemical analysis was then performed using gas chromatography-mass spectrometry (GC–MS). Monoterpenes and sesquiterpenes were identified by comparing retention times of known standards and mass spectra using the NIST library and MSD Chemstation software. Concentrations for each compound were calculated using five-point calibration curves with injections of known amounts of pure standards and the internal standard, fenchone. When pure standards were unavailable, standard curves for (–)-α-pinene, terpinolene, bornyl acetate, and caryophyllene were used for monoterpenes, oxygenated monoterpenes, monoterpene esters and sesquiterpenes, respectively. For unidentified compounds, putative NIST IDs were used when match quality was greater than 80.

2.6. Data analysis

All analyses were conducted using R (v. 3.5.0) (R Development Core Team 2008). We used Wilcoxson paired *t*-tests, linear regression, correlation, and multivariate analyses of variance to investigate relationships in growth and defense anatomy, as well as constitutive resin chemistry, across lodgepole and whitebark pine pairs. We evaluated significance using one-tailed tests for *a priori* expectations described in the Introduction (e.g., higher concentrations of terpenes, greater duct size, greater duct production, etc.) and two-tailed tests for all other tests using $\alpha = 0.05$.

It is currently unclear how long resin ducts in conifers remain biologically active and contribute to constitutive and induced resin chemistry (Trapp and Croteau 2001). As such, we measured growth and defense metrics over the full record (1914–2018) as well as over the most recent 20-years (1998–2018), and 5-years (2013–2018) prior to sampling. We applied a Bonferroni correction factor ($\alpha = 0.05/3 = 0.017$) for all growth periods to account for multiple comparisons across similar growth intervals. From the raw tree ring width data we used the *dplR* package (v. 1.7.1) (Bunn 2008) to calculate cross-sectional basal area increments (BAI; mm^2 $year^{-1}$) as an approximate indicator of volumetric growth over time (Biondi and Qeadan 2008).

For mono- and sesqui- terpenes, we standardized concentrations by phloem mass (g) to calculate absolute concentration (μg / g phloem) for each compound. We then summed the concentrations for all identified compounds to obtain total concentration (41 identified monoterpenes and 39 identified sesquiterpenes). For individual compounds, we calculated the relative concentration of each as percent of the total concentration. A one-way Welch's ANOVA was used to test for a species effect on total mono- and sesqui- terpenes, followed by a Tukey's honest significant difference test (HSD) *post-hoc* to identify pairwise differences between species. Due to non-normally distributed data, mono- and sesqui- terpene amounts were either square root or log-transformed for these analyses. Mono- and sesqui- terpene diversity was calculated as the Shannon diversity index (*H'*), a measure of within-sample diversity. We also used non-metric multidimensional scaling (NMDS) to explore mono- and sesqui- terpene dissimilarity between the two species (Kenkel and Orlóci 1986, Dixon 2003). Dissimilarity for the NMDS ordination was calculated using the *betadisper* function in the *vegan* package (v. 2.5–6) in R (Dixon 2003).

To assess the role of competition we summed basal area (m^2) for each species of competitor and for all trees sampled around each focal tree to a maximum distance of 10 m (Fig. S2). From these data we calculated stand density index (SDI) (Reineke 1933) for each tree and developed generalized linear models to assess whether local competition and/or canopy position, influence constitutive levels of mono- and sesqui- terpenes and/or growth and resin duct anatomy. All models were compared using Akaike information criterion (AIC) (Burnham et al. 2010).

3. Results

3.1. Relationship between constitutive resin chemistry and resin ducts

Whitebark and lodgepole pines at our study site were similar in terms of size (diameter and height), age, and growth (Table 1). In general, tree size, tree growth, and resin duct properties correlated poorly with constitutive mono- and sesqui- terpenes in both species. However, across the full time-series (1914–2018) resin duct area was positively correlated with monoterpenes ($r = 0.44$, $p = 0.0152$) and sesquiterpenes ($r = 0.44$, $p = 0.0150$) in whitebark pine only (Table 2). This held true for whitebark pine duct area and sesquiterpenes over the 20-years prior to sampling ($r = 0.48$, $p = 0.0079$) but not over the 5-years prior to sampling (Table S2). Whitebark pine resin duct size also tended to be correlated positively with sesquiterpenes across the full record ($r = 0.41$, $p = 0.0127$; Table 2) and over the 20-years prior to sampling ($r = 0.45$, $p = 0.0069$) but not over the 5-years prior to sampling (Table S2).

Resin duct production was positively correlated with monoterpenes in whitebark pine ($r = 0.43$, $p = 0.0095$) across the full time-series but showed no relationship in lodgepole pine (Table 2). We did not detect relationships between constitutive mono- and sesqui- terpenes and resin duct density, relative duct area, growth (BAI), or tree size (DBH) for either species (Table 2).

3.2. Chemical composition of constitutive resin in trees

Whitebark pine contained 31% greater abundance (μg / g of sample tissue) of constitutive monoterpenes ($p = 0.0193$; Fig. 2A) and 68%

Table 1
Mensuration data (mean ± S.E.) for 30 whitebark pine (*P. albicaulis*) and 30 lodgepole pine (*P. contorta* var. *latifolia*) sampled at a high elevation montane site on the Flathead Indian Reservation in northwestern Montana.

	Pinus albicaulis	*Pinus contorta*
Age (years)	92.2 (±2.11)	88.6 (±1.78)
DBH (cm)	24.2 (±0.81)	24.5 (±0.84)
Height (m)	20.2 (±1.31)	21 (±1.3)
Live Crown Ratio (%)	73 (±0.02)	74 (±0.02)
Aspect (°)	188.5 (±13.02)	177.1 (±12.48)
BAI (cm^2 $year^{-1}$)	523.7 (±50.11)	486.7 (±42.55)
Duct Production (no. $year^{-1}$)	3.2 (±0.16)	2.9 (±0.1)
Duct Size (mm^2)	0.021 (±0.001)	0.024 (±0.001)
Duct Area (mm^2 $year^{-1}$)	0.038 (±0.002)	0.039 (±0.002)
Duct Density (no. mm^{-2} $year^{-1}$)	0.85 (±0.1)	0.78 (±0.08)
Relative Duct Area (% annual ring)	0.92 (±0.05)	1.03 (±0.06)

Note: DBH = diameter at breast height; BAI = basal area increment

Table 2
Spearman correlation coefficients of mono- and sesqui- terpene concentrations (μg / g fresh weight) with tree ring growth and resin duct anatomical measurements in whitebark (*P. albicaulis*) and lodgepole pine (*P. contorta* var. *latifolia*). Correlations were conducted on metrics averaged over the full time series (1914–2018).

	Monoterpenes		**Sesquiterpenes**	
	Pinus albicaulus	*Pinus contorta*	*Pinus albicaulus*	*Pinus contorta*
DBH	0.13	0.19	0.28	0.21
Growth (BAI)	0.18	0.24	0.24	0.1
Duct Production	**0.43**	–0.1	0.23	–0.18
Duct Size	0.26	0.34	**0.41**	0.18
Duct Area	**0.44**	0.28	**0.44**	0.06
Duct Density	0.35	–0.18	–0.06	–0.2
Relative Duct Area	0.33	–0.13	0.003	–0.22

Note: Bold values indicate significant correlations ($p < 0.017$). DBH = diameter at breast height; BAI = basal area increment.

greater abundance of constitutive sesquiterpenes ($p < 0.0001$; Fig. 2B) compared to lodgepole pine. The diversity (H') of constitutive monoterpenes did not differ significantly between whitebark and lodgepole pine (Fig. S3A). Unlike monoterpenes, constitutive sesquiterpene diversity was greater in whitebark pine compared to lodgepole pine ($p < 0.0001$; Fig. S3B). Generally, mono- and sesqui- terpene diversity was unrelated to tree growth and resin duct anatomy. However, in whitebark pine, monoterpene diversity was positively related to resin duct production over the full 104-year record ($r = 0.43$, $p = 0.0092$; Table S3).

We identified 22 monoterpenes that differed considerably across the two species (Fig. 3A, Table S4). Specifically, we found 5.96x greater (–)-α-pinene, 8.2x greater (+)-α-pinene, 4.5x greater β -myrcene, and 2.5x greater (+)-β -pinene in whitebark pine (Table S4). Whitebark also had greater quantities of β -ocimene (92.8x higher), γ-terpinene (3.4x higher), anisole (9.9x higher), α-longipinene (7.7x higher), ρ-cymene (36.2x higher), cis- β -terpineol (5x higher), 3-carene (3x higher), and two unidentified monoterpenes: MTP 6 (6x higher) and MTP 9 (4.3x higher; Table S4). In contrast, lodgepole pine exhibited greater concentrations of α-phellandrene (6.8x higher), β -phellandrene (1.4x higher), dill ether (32.4x higher), (+)-linalool (1.8x higher), and an unidentified monoterpene (MTP 3; 1.7x higher). There were also more nuanced differences regarding some compounds. For instance, lodgepole pine contained greater concentrations of (–)-sabinene (4.8x higher), while whitebark contained 15.7x more of the stereoisomer (+)-sabinene (Table S4). Similarly, whitebark contained 4.8x more of (–)-δ-limonene, while lodgepole contained 5.7x more of the stereoisomer (+)-δ-limonene (Fig. 3A, Table S4). Lodgepole pine also produced more of the phenolic phenylpropanoid 4-allylanisole (10.1x higher) than whitebark pine (Fig. 3A, Table S4).

We identified 33 sesquiterpenes that were significantly different between whitebark and lodgepole pine (Fig. 3B, Table S4). Whitebark pine contained greater quantities (raw concentrations and percent composition) for 73% of these, while lodgepole pine contained greater quantities of α-cadinol (1.5x higher), and seven unknown sesquiterpenes (SQT 4, SQT 6, SQT 8, SQT 9, SQT 11, SQT 14, SQT 15) (Fig. 3B, Table S4).

3.3. Relationships between tree growth and resin ducts in whitebark and lodgepole pine

Overall, the variables describing growth and resin duct properties were similar between the two species (Table 1). Tree size (DBH), height, and growth (BAI) were similar as was resin duct production, duct area, duct density, and relative duct area. However, across the full time series (1914–2018) lodgepole pines produced 10% larger resin ducts on average relative to whitebark pine ($p = 0.0033$; Fig. 4).

Unstandardized resin duct metrics (size, area, and production) correlated positively with growth (BAI) for both species, while standardized duct metrics (duct density and relative duct area) correlated negatively with growth. Specifically, resin duct production showed a strong positive correlation with growth for whitebark pine ($r = 0.59$, $p = 0.0007$; Fig. S4A) but not for lodgepole pine (Table 3). Resin duct size and growth were positively correlated for both whitebark pine ($r = 0.52$, $p = 0.0034$) and lodgepole pine ($r = 0.56$, $p = 0.0014$; Fig. S4B). Similarly, resin duct area and growth were strongly, positively correlated for whitebark ($r = 0.71$, $p < 0.00001$) and lodgepole ($r = 0.55$, $p = 0.0016$; Table 3, Fig. S4C). In contrast, resin duct density and growth were negatively correlated for whitebark pine ($r = –0.36$, $p = 0.0539$) and lodgepole pine ($r = –0.55$, $p = 0.0019$; Table 3, Figure S4D). Relative duct area was also negatively correlated with growth for whitebark pine ($r = –0.6$, $p = 0.0005$) and lodgepole pine ($r = –0.61$, $p = 0.0004$; Table 3, Fig. S4E).

Tree size (DBH) was positively correlated with growth (BAI) for both lodgepole ($r = 0.69$, $p < 0.0001$) and whitebark pine ($r = 0.77$, $p < 0.0001$; Table 3). In whitebark pine, tree size was also positively correlated with resin duct production ($r = 0.39$, $p = 0.0352$), duct size ($r = 0.46$, $p = 0.0098$), and duct area ($r = 0.56$, $p = 0.0014$; Table 3). Tree size was negatively correlated with resin duct density in whitebark pine ($r = –3.7$, $p = 0.04215$) and relative duct area in lodgepole ($r = –0.45$, $p = 0.01179$) and whitebark pine ($r = –0.58$, $p = 0.0008$; Table 3).

3.4. Relationship of overstory competition and constitutive resin chemistry

Stand density index (SDI) was not correlated with tree size, tree growth, nor resin duct metrics for both species (Table 4). SDI was also

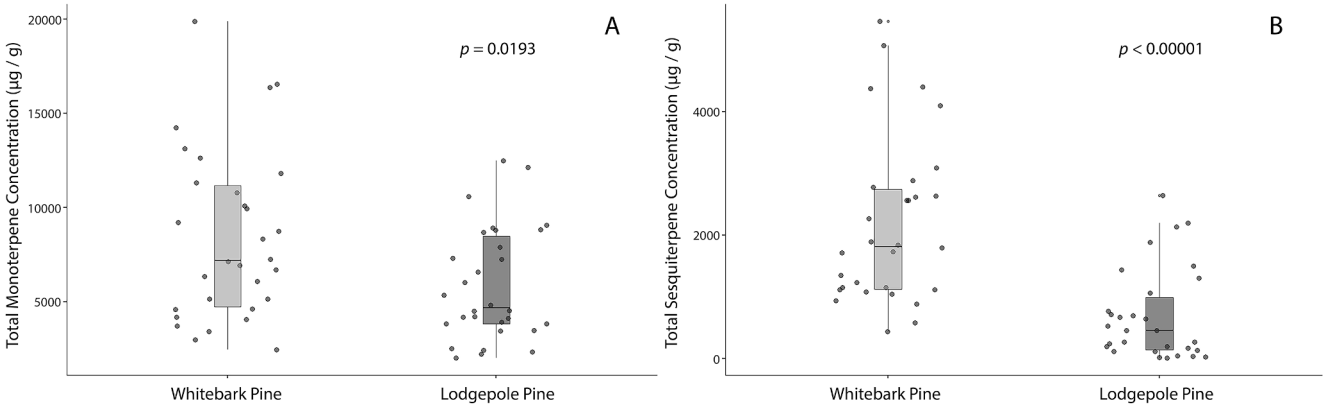

Fig. 2. Comparison of total constitutive concentrations (μg / g fresh weight) of monoterpenes (A) and sesquiterpenes (B) across 30 whitebark pine (*P. albicaulis*) and 30 lodgepole pine (*P. contorta*).

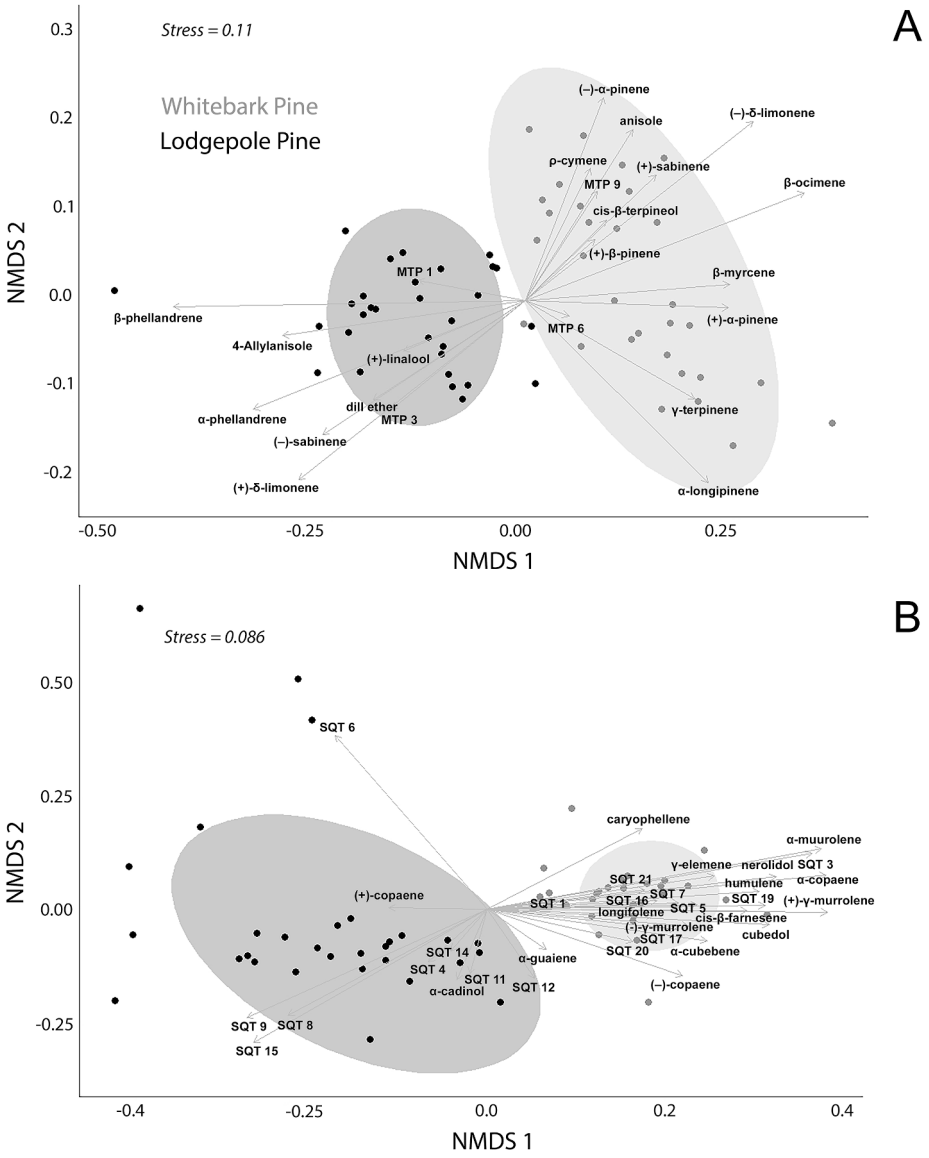

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination plot of the first and second dimensions for the A) monoterpene and B) sesquiterpene profiles of 30 whitebark pine and 30 lodgepole pine trees. Ellipses represent a 99% confidence interval for each species. Important individual monoterpenes are overlain with the relative magnitude of the arrows corresponding to their respective importance in the ordination.

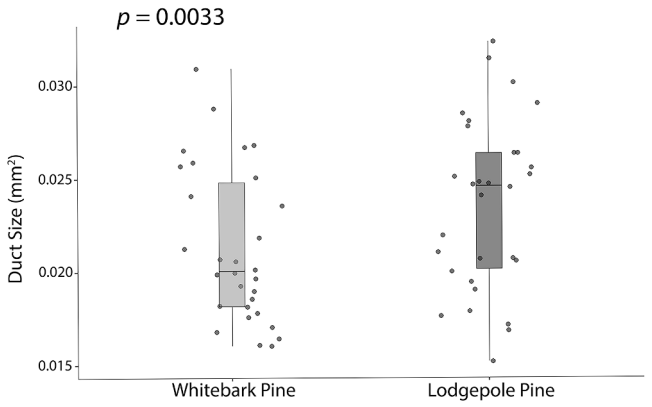

Fig. 4. Comparison of resin duct size across the full time series (1914–2018).

not correlated with constitutive mono- nor sesqui- terpenes for lodgepole pine (Table 4). However, in whitebark pine there was a significant negative correlation between monoterpenes and SDI (r = –0.38, p = 0.0179; Table 4), indicating monoterpene concentrations declined with increasing stand density.

Lodgepole pine basal area comprised approximately 55% of near-tree competition (average DBH = 24.8 cm ± 0.77), followed by whitebark pine (25%, average DBH = 15.3 cm ± 0.8), subalpine fir (12%, average DBH = 14.5 cm ± 1), Engelmann spruce (5%, average DBH = 19.3 cm ± 1.9), and Douglas-fir (3%, average DBH = 22.7 cm ± 4.7). Engelmann spruce was consistently in the top performing models predicting constitutive monoterpenes as a function of near-tree competition (Table 5). In addition, constitutive mono- and sesqui- terpene concentrations in whitebark pine were negatively affected by near-tree competition with Engelmann spruce (p = 0.0227) while no relationships were found for lodgepole pine (Table S5). Generally, constitutive levels of monoterpenes in whitebark pine decreased with increasing Engelmann spruce basal area.

Table 3
Spearman correlation coefficients of tree ring growth and resin duct anatomical measurements of *Pinus contorta* and *Pinus albicaulis*. Correlations were conducted on metrics averaged over the full time series (1914–2018).

Pinus albicaulis	**DBH**	**Growth (BAI)**	**Duct Production**	**Duct Size**	**Duct Area**	**Duct Density**	**Relative Duct Area**
Growth (BAI)	**0.77**						
Duct Production	**0.39**	**0.59**					
Duct Size	**0.46**	**0.52**	0.11				
Duct Area	**0.56**	**0.71**	**0.63**	**0.84**			
Duct Density	**–0.37**	**–0.36**	**0.36**	**–0.48**	–0.17		
Relative Duct Area	**–0.58**	**–0.6**	0.01	–0.34	–0.24	**–0.85**	
Pinus contorta							
Growth (BAI)	**0.69**						
Duct Production	0.12	0.08					
Duct Size	0.25	**0.56**	–0.06				
Duct Area	0.24	**0.55**	**0.36**	**0.9**			
Duct Density	–0.35	**–0.55**	0.25	**–0.62**	**–0.45**		
Relative Duct Area	**–0.45**	**–0.61**	0.14	–0.32	–0.22	**0.87**	

Note: Bold values indicate significant correlations ($p < 0.05$). DBH = diameter at breast height; BAI = basal area increment.

Table 4
Spearman correlation coefficients of stand density (Reineke's Stand Density Index; SDI), tree size (DBH), tree ring growth (BAI), and resin duct anatomical measurements for whitebark (*P. albicaulis*) and lodgepole pine (*P. contorta* var. *latifolia*). Correlations were conducted on metrics averaged over the full time series (1914–2018).

	Stand Density Index (SDI)	
	Pinus albicaulis	*Pinus contorta*
Monoterpene concentration	**–0.38**	0.09
Sesquiterpene concentration	–0.29	–0.24
Monoterpene Diversity (*H'*)	–0.26	0.16
Sesquiterpene Diversity (*H'*)	–0.24	–0.34
DBH	–0.05	–0.09
Growth (BAI)	–0.05	–0.28
Duct Production	0.01	–0.05
Duct Size	–0.17	–0.33
Duct Area	–0.15	–0.33
Duct Density	–0.05	0.35
Relative Duct Area	–0.22	0.28

Note: Bold values indicate significant correlations ($p < 0.05$). DBH = diameter at breast height; BAI = basal area increment.

Table 5
Generalized linear models predicting constitutive monoterpenes as a function of overstory competition. Log likelihood reflects the probability of the data given the model, while K represents the relative number of sample parameters for each model. Top five models are shown as well as intercept-only model for reference. (↑) indicates a positive coefficient in the model while (↓) indicates a negative coefficient.

Model	**AICc**	**ΔAIC**	**LogL**	**K**
1. SPC (↑) + PIEN (↓) + PSME (↓) + PICO (↑) + [PIEN * SPC] (↓) + [PICO * SPC] (↓)	1159.6	0.00	–570.39	6
2. SPC (↑) + PIEN (↓) + PSME (↓) + [PIEN * SPC] (↓)	1160.7	1.12	–573.57	4
3. SPC (↑) + PIEN (↓) + [PIEN * SPC] (↓)	1161.3	1.69	–575.09	3
4. SPC (↑) + PIEN (↓) + PSME (↓) + PICO (↑) + [PIEN * SPC] (↓) + [PSME * SPC] (↓) + [PICO * SPC] (↓)	1161.3	1.75	–569.87	7
5. SPC (↑) + PIEN (↓) + PSME (↓) + PICO (↑) + ABLA (↓) + [PIEN * SPC] (↓) + [PICO * SPC] (↓)	1161.8	2.21	–570.10	7
6. Intercept-Only Model	1168.8	9.2	–582.28	1

Abbreviations: SPC (species), PIEN (Engelmann spruce competitors), PSME (Douglas-fir competitors), PICO (lodgepole pine competitors), ABLA (subalpine fir competitors).

4. Discussion

Our 104-year record comparing growth and defense characteristics within and between whitebark and lodgepole pine yields four important findings. First, we did not find evidence of a tradeoff between tree growth and tree defenses (resin duct morphology and resin chemistry; Table 2, S2). This suggests that trees growing under favorable field conditions can experience high growth rates and be well defended. Second, we found that resin duct size, production, and area are not related to constitutive mono- and sesqui- terpene concentrations in lodgepole pine, whereas resin duct production and area were positively related to constitutive monoterpenes, and resin duct size and area were positively related to constitutive sesquiterpenes, in whitebark pine (Table 2, S2). The lack of distinct, universal relationships between these defensive features presents beetles with numerous and unpredictable combinations of resin-based defenses, particularly from its historical host, lodgepole pine (Mason et al. 2019, Howe et al. 2020). Third, based on constitutive terpene profiles, bark beetles are more likely to enter lodgepole pine but more likely to successfully elicit mass attacks in whitebark pine, which agrees with beetle attack and success patterns in the field (Fig. 3) (Bentz et al. 2015). Fourth, overstory competition, particularly by Engelmann spruce, can influence tree defenses, specifically constitutive terpene concentrations (Table 5, S5). Competitive tree interactions could lead to altered bark beetle-conifer interactions as host and nonhost species migrate in response to changing climate. This is particularly relevant within montane environments, where climate-related tree species migration could occur more rapidly (elevational range shifts over hundreds of meters) compared to flatter regions (latitudinal range shifts over hundreds of kilometers).

Overall, relationships between growth and defense in lodgepole and whitebark pine were relatively similar (Table 3). Counter to our hypothesis (H_1), we did not find evidence to suggest that trees producing more and larger resin ducts also have higher concentrations and diversity of mono- and sesqui- terpenes. In contrast, whitebark pine trees produced smaller resin ducts structures than lodgepole pine (Fig. 4) but also had greater constitutive levels of mono- and sesqui- terpenes (Fig. 2). These findings differ from results in the Greater Yellowstone Ecosystem reporting greater duct production and greater levels of constitutive monoterpenes and diterpenes in lodgepole pine than whitebark pine but are similar in both showing higher sesquiterpenes in whitebark pine (Fig. S3) (Raffa et al. 2013, Raffa et al. 2017, Mason et al. 2019). In addition, resin duct area positively correlated with constitutive mono- and sesqui- terpenes for whitebark pine, but not in lodgepole pine, suggesting that whitebark pines with increased resin duct area also have greater concentrations of constitutive mono- and sesqui- terpenes (Table 2, S2). This is supported by research demonstrating that, in some species, increased resin duct area is positively related to resin flow (Hood and Sala 2015, Yi et al. 2021). Duct area also correlated strongly

with tree size (DBH) and growth (BAI) in whitebark pine (Table 3), which could assist managers in the identification of candidate trees for silvicultural treatments and/or seed collection efforts (Table 3). Counter to our hypothesis (H_2) relative duct area was not related to constitutive mono- and sesqui- terpene concentrations for either species (Table 2). Lodgepole pine had greater relative duct area than whitebark pine but lower levels of constitutive mono- and sesqui- terpenes (Fig. 2). In addition, sesquiterpene diversity was lower in lodgepole pine than whitebark pine while we did not detect significant difference in monoterpene diversity between the two species (Fig. S3).

Interestingly, we did not detect significant tradeoffs in the allocation of resources between tree growth and investment in resin duct structures and constitutive mono- and sesqui- terpenes. Rather, we found generally positive relationships between tree size and growth versus unstandardized resin duct metrics and constitutive mono- and sesqui- terpenes (Table 2, S2). This likely reflects the highly variable site quality of natural forest stands rather than an absence of within-plant allocation posited by Herms and Mattson (1992). That is, within-plant allocation patterns do not necessarily scale up to between-plant inverse relationships (and may even be reversed) at the landscape scale (Howe et al. 2020). This view has some support, as Waring and Pitman (1985), Bleiker et al. (2005), Knapp et al. (2013), Williams et al. (2018) and Keen et al. (2020) found that fast-growing trees were most likely to survive bark beetle outbreaks. However, other research has demonstrated the opposite, whereby slower growing trees were more likely to persist through increased beetle activity (de la Mata et al. 2017, Reed and Hood 2020). Investment in plant growth and defense is nuanced and changes across geographic environments and microclimates, as well as with plant ontogeny, stand dynamics and seasonality. Given the numerous physiological mechanisms modulating tree growth and the expression of defensive features, more research is needed to better understand if and how these relationships differ across broader ecological and temporal scales.

We interpret the lack of clear relationships among tree growth, resin duct morphology and resin chemistry as part of complex evolutionary processes shaping bark beetle-host interactions. While mountain pine beetles have evolved to exploit chemical signatures in the identification and colonization of individuals, trees present bark beetles with innumerable permutations of physical and chemical defenses (Mason et al. 2019). A beetle cannot readily predict resin duct architecture during host identification and colonization. Thus, trees with well-developed resin duct defenses have an advantage of enduring bark beetle attack. This is supported by research demonstrating the importance of resin duct anatomy in surviving beetle activity for a variety of conifers (Vázquez-González et al. 2020). For instance, Kichas et al. (2020) found that whitebark pine that persisted through stand-level beetle activity produced fewer but larger resin ducts with greater resin duct area and greater relative duct area than whitebark pine that died. Similar results have been reported for lodgepole pine (Ferrenberg et al. 2014, Zhao and Erbilgin 2019), ponderosa pine (Kane and Kolb 2010, Hood et al. 2015), limber pine (Ferrenberg et al. 2014, Bentz et al. 2017), maritime pine (*P. pinaster*) (Zas et al. 2014), foxtail pine (*P. balfouriana*) and Great Basin bristlecone pine (*P. flexilis*) (Bentz et al. 2017). Likewise, the composition and quantities of resin chemistry, both constitutive and induced, can mediate tree survival from bark beetles (Raffa et al. 2005, Zhao et al. 2011, Erbilgin et al. 2017). There is also evidence to suggest that insect activity can shape growth and resin-based defenses directly in lodgepole pine (Zhao et al. 2019) and ponderosa pine (de la Mata et al. 2017). However, the myriad interacting factors influencing tree defenses complicates our ability to generalize relationships across species or make assumptions about resin duct characteristics and beetle interactions. More work is needed to understand the many biotic and abiotic processes modulating tree growth and development of resin-based defenses, specifically relating to climate, stand dynamics, and disturbance histories.

4.1. Constitutive resin chemistry

We found clear species-level differences in the composition of mono- and sesqui- terpenes between whitebark and lodgepole pine (Fig. 3, Table S4). These differences relate to mountain pine beetle behavior and attack success and largely agree with other research (Raffa et al. 2013, Raffa et al. 2017). In support of H_3, whitebark pine produced greater quantities of compounds known to enhance beetle success, including (–)-α-pinene, which beetles use as precursor for the biosynthesis of their aggregation pheromone, (–)-*trans*-verbenol (Blomquist et al. 2010, Keeling 2016). Whitebark also produced more β-myrcene, which mountain pine beetles utilize as synergists for pheromone attraction (Borden et al. 2008). While lodgepole pine produced less of these compounds we found significantly greater levels of α–phellandrene and β–phellandrene, which mountain pine beetles exploit for host recognition. Lodgepole pine also produced more compounds that inhibit beetle fitness, including (+)-δ-limonene, which is highly toxic to mountain pine beetles, and 4-allylanisole (aka estragole), which inhibits attraction to pheromones (Hayes and Strom 1994). Thus, despite having fewer exploitable compounds for pheromone production and enhancement, the increased concentration of compounds important for host recognition likely results in mountain pine beetles identifying lodgepole pines for colonization over co-occurring whitebark pine under endemic beetle activity. However, under mass attack and outbreak scenarios, beetles are more likely to succeed when colonizing whitebark pine trees. As beetle activity is projected to increase with increasing temperatures, particularly at higher elevations, the implications for whitebark pine mortality are concerning and may warrant management actions to mitigate potential loss of this important species.

We found some evidence for our hypothesis (H_4) as lodgepole pine produced larger resin ducts with greater relative duct area compared to whitebark pine; however, counter to our hypothesis, lodgepole pine had lower levels of constitutive terpenes (Figs. 2, 4). We do not interpret the lack of relationship between resin duct anatomy and constitutive resin chemistry in lodgepole pine as an indication that lodgepole pine are any less defended against bark beetles than whitebark pine. There are many factors, such as climate, soil quality, tree size / age, stand dynamics, and disturbance histories, that can influence tree physiology and defense anatomy in conifers. For instance, the chemical composition of oleoresin can change dramatically when trees are exposed to fungi vectored by bark beetles (Keefover-Ring et al. 2016). Notably, our results only pertain to constitutive chemical defenses. While there is a growing body of literature investigating constitutive and inducible defenses, more work is needed to better understand the relationship of constitutive and inducible defenses within and across species, as well as ecological implications of these relationships (Howe et al. 2020). In addition, the potential ecological roles of sesquiterpenes in beetle-conifer-microbial interactions are unknown. Sesquiterpenes can play a role in cold tolerance in some plants (Zhao et al. 2020), which is consistent with their higher abundance in the high elevation whitebark pine, but again such a function has not been tested in pines. More work is needed to understand how these compounds vary across species and environments and what functions they may serve in conifer defense.

4.2. Influence of competition on tree defense

Trees sampled for this study were relatively young (90 year mean age) (Reed et al. 2018) and growing in a moderately dense lodgepole pine-dominant, mixed-conifer forest stand in the northern Rocky Mountains. We hypothesized that competition in this setting would reduce nutrient availability, limiting the overall capacity for trees to produce primary and secondary metabolites. We found some support for this hypothesis (H_5), as stand density (SDI) was negatively correlated with constitutive monoterpene concentrations for whitebark pine (Table 4). Also, the frequency of relationships having a negative although statistically insignificant relationships suggests that additional

studies into whether increased competition reduces growth and defense in whitebark and lodgepole pine is warranted. Future studies providing greater spatial and temporal resolution and more explicitly directed design may reveal ecologically meaningful insights into the role of local competition.

We did not detect notable influence of inter- or intra- specific competition on constitutive terpene abundance or diversity (Table S5). However, we did find evidence that Engelmann spruce interacts with whitebark pine, resulting in decreased monoterpene concentrations with increasing Engelmann spruce presence (Table 5, S5). This trend was observed in whitebark pine despite Engelmann spruce occupying a small percentage of local competition (5%). In addition, Engelmann spruce was a comparatively strong predictor of constitutive monoterpenes in whitebark pine compared to other competitors (Table 5). This merits further investigation because as climate warms and different tree species migrate along elevational and/or latitudinal gradients they may increasingly encounter species, such as Engelmann spruce, that could negatively influence their defenses. This could have important implications for management and conservation efforts, particularly given projected increases in both temperature and mountain pine beetle activity in the western U.S. over the next century (Bentz et al. 2016, Buotte et al. 2016, 2017).

Whether these effects are attributable to the microsites where Engelmann spruce resides or to more nuanced direct and indirect effects of Engelmann spruce ecology (e.g., changes in soil characteristics through litter deposition, root exudates, and unique microbial assemblages) remains unclear. It is also possible that other tree-level factors, such as tree height and canopy vigor, could influence these relationships, as taller trees with more photosynthetically active canopies may be superior competitors for light and limiting nutrients. While we only assessed diameter and species information for competitor trees, we recommend that future studies investigating the role of competition on conifer defenses also consider other aspects of tree growth and function. Understanding the degree to which competition and/or differences in site characteristics influence constitutive and induced resin-based defenses will enable managers to modify prescriptions to better achieve desired objectives.

4.3. Conclusions

We found differences in whitebark and lodgepole pine growth and physical / chemical defenses that have important implications for bark beetle behavior and forest management. Importantly, we did not detect tradeoffs between tree growth and constitutive resin-based defenses, indicating that trees at this site are both growing fast and well defended. Second, tree growth, resin duct architecture, and resin chemistry are largely unrelated. The lack of relationships between these different factors presents beetles with many permutations of resin-based defenses that can address the multitude of contexts under which attacks occur. Third, whitebark pine contains greater levels of constitutive compounds known to enhance bark beetle behavior and success, while lodgepole pine contains greater concentrations of compounds known to increase host recognition. Lastly, our record suggests that interspecific competition, particularly with Engelmann spruce, can influence constitutive resin chemistry. This may in turn increase susceptibility to mountain pine beetle, yielding unexpected challenges in whitebark pine conservation and restoration efforts.

These results have several important implications. From the perspective of a bark beetle, whitebark pine appear more chemically conducive for reproductive success while lodgepole pine are more identifiable as potential hosts. Under endemic scenarios mountain pine beetle persist in low numbers, colonizing stressed individuals with depleted defense systems. However, during outbreak conditions, beetle populations can overwhelm defenses of vigorous, well-defended trees. As such, even the healthiest whitebark pine growing within this mixed-conifer setting may be vulnerable to beetle-induced mortality. However, conifers have co-evolved with insects and have developed complex defensive strategies in response to these pressures. Resin duct architecture can facilitate oleoresin production and mobilization in ways that are not readily perceptible to beetles. The lack of clear relationships between these various defensive features reflects the complexity of the biophysical relationships connecting them. In addition, local competition and species-specific interactions may further influence growth and defense characteristics, leading to unpredictable outcomes as species migrate in response to a warming climate.

Changing forest conditions are confronting managers with increasingly limited options for preserving and promoting whitebark pine populations. Many management prescriptions rely on superficial performance indicators (primarily growth) that fail to account for the important role of physical and chemical defenses in moderating disturbance interactions. Few studies have investigated patterns of growth and defense using multiple proxies (resin duct anatomy and resin chemistry), so there is a need to expand this research to a broader range of species and environments.

CRediT authorship contribution statement

Nickolas E. Kichas: Conceptualization, Investigation, Formal analysis, Methodology, Visualization, Writing - original draft, Funding acquisition. **Amy M. Trowbridge:** Conceptualization, Investigation, Formal analysis, Methodology, Resources, Writing - review & editing. **Kenneth F. Raffa:** Investigation, Supervision, Writing - review & editing. **Shealyn C. Malone:** Formal analysis, Investigation, Writing - review & editing. **Sharon M. Hood:** Conceptualization, Investigation, Methodology, Writing - review & editing. **Richard G. Everett:** Project administration, Resources. **Gregory T. Pederson:** Resources, Writing - review & editing. **David B. McWethy:** Conceptualization, Methodology, Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119286.

References

Amberson, J., Keville, M., Nelson, C., 2018. Effects of Disturbance on Tree Community Dynamics in Whitebark Pine (Pinus albicaulis Engelm.) Ecosystems. Forests 9 (566).
Anderson, M.D., 2003. Pinus contorta var. latifolia. Fire Effects Information System. U.S. D.A. Forest Service, Fire Sciences Laboratory.
Arno, S.F., Hoff, R.J., 1989. Silvics of Whitebark Pine (Pinus albicaulis). In: F. S. United States Department of Agriculture, (Ed.) Lntermountain Research Station, Ogden, UT.

Baker, W.L., 2009. Fire Ecology in Rocky Mountain Landscapes, 1 edition. Island Press, Washington, D.C.
Bentz, B.J., Boone, C., Raffa, K.F., 2015. Tree Response and Mountain Pine Beetle Attack Preference, Reproduction and Emergence Timing in Mixed Whitebark and Lodgepole Pine Stands. Agric. For. Entomol. 17, 421–432.
Bentz, B.J., Duncan, J.P., Powell, J.A., 2016. Elevational Shifts in Thermal Suitability for Mountain Pine Beetle Population Growth in a Changing Climate. Forestry 89, 271–283.
Bentz, B.J., Hood, S.M., Hansen, E.M., Vandygriff, J.C., Mock, K.E., 2017. Defense Traits in the Long-Lived Great Basin Bristlecone Pine and Resistance to the Native Herbivore Mountain Pine Beetle. New Phytol. 213, 611–624.
Biondi, F., Qeadan, F., 2008. A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Research 64, 81–96.
Bleiker, K.P., Staffan Lindgren, B., Maclauchlan, L.E., 2005. Resistance of Fast- and Slow-Growing Subalpine Fir to Pheromone-Induced Attack by Western Balsam Bark Beetle (Coleoptera: Scolytinae). Agric. For. Entomol. 7, 237–244.
Blomquist, G.J., Figueroa-Teran, R., Aw, M., Song, M., Gorzalski, A., Abbott, N.L., Chang, E., Tittiger, C., 2010. Pheromone Production in Bark Beetles. Insect Biochem. Mol. Biol. 40, 699–712.
Boone, C.K., Keefover-Ring, K., Mapes, A.C., Adams, A.S., Bohlmann, J., Raffa, K.F., 2013. Bacteria Associated with a Tree-Killing Insect Reduce Concentrations of Plant Defense Compounds. J. Chem. Ecol. 39, 1003–1006.
Borden, J.H., Pureswaran, D.S., Lafontaine, J.P., 2008. Synergistic Blends of Monoterpenes for Aggregation Pheromones of the Mountain Pine Beetle (Coleoptera: Curculionidae). J. Econ. Entomol. 101, 1266–1275.
Bunn, A.G., 2008. A Dendrochronology Program Library in R (dplR). Dendrochronologia 26, 115–124.
Buotte, P.C., Hicke, J.A., Preisler, H.K., Abatzoglou, J.T., Raffa, K.F., Logan, J.A., 2016. Climate Influences on Whitebark Pine Mortality from Mountain Pine Beetle in the Greater Yellowstone Ecosystem. Ecol. Appl. 26, 2507–2524.
Buotte, P.C., Hicke, J.A., Preisler, H.K., Abatzoglou, J.T., Raffa, K.F., Logan, J.A., 2017. Recent and Future Climate Suitability for Whitebark Pine Mortality from Mountain Pine Beetles Varies Across the Western U.S. For. Ecol. Manage. 399, 132–142.
Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2010. AIC Model Selection and Multimodel Inference in Behavioral Ecology: Some Background, Observations, and Comparisons. Behav. Ecol. Sociobiol. 65, 23–35.
Celedon, J.M., Bohlmann, J., 2019. Oleoresin Defenses in Conifers: Chemical Diversity, Terpene Synthases and Limitations of Oleoresin Defense Under Climate Change. New Phytol.
Chiu, C.C., Keeling, C.I., Bohlmann, J., 2019. The Cytochrome P450 CYP6DE1 Catalyzes the Conversion of Alpha-Pinene into the Mountain Pine Beetle Aggregation Pheromone Trans-Verbenol. Science Reports 9, 1477.
Coomes, D.A., Grubb, P.J., 2000. Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments. Ecol. Monogr. 70, 171–207.
CSKT, 2000. Flathead Indian Reservation Forest Management Plan. In: Forestry, T., (Ed.) Confederated Salish and Kootenai Tribes, Pablo, MT, p. 304.
CSKT, 2007. Flathead Indian Reservation Fire Management Plan. In: Management, D.o. F., (Ed.) Confederated Salish and Kootenai Tribes, Ronan, MT, p. 115.
de la Mata, R., Hood, S.M., Sala, A., 2017. Insect Outbreak Shifts the Direction of Selection from Fast to Slow Growth Rates in the Long-Lived Conifer Pinus ponderosa. Proc. Natl. Acad. Sci. 114, 7391–7396.
Dixon, P., 2003. VEGAN, a Package of R Functions for Community Ecology. J. Veg. Sci. 14, 927–930.
Duhl, T.R., Gochis, D., Guenther, A.B., Ferrenberg, S., Pendall, E., 2013. Emissions of BVOC from Lodgepole Pine in Response to Mountain Pine Beetle Attack in High and Low Mortality Forest Stands. Biogeosciences 10, 483–499.
Erbilgin, N., Cale, J.A., Hussain, A., Ishangulyyeva, G., Klutsch, J.G., Najar, A., Zhao, S., 2017. Weathering the Storm: How Lodgepole Pine Trees Survive Mountain Pine Beetle Outbreaks. Oecologia 184, 469–478.
Erbilgin, N., Raffa, K.F., 2001. Modulation of Predator Attraction to Pheromones of Two Prey Species by Stereochemistry of Plant Volatiles. Oecologia 127, 444–453.
Ferrenberg, S., Kane, J.M., Langenhan, J.M., 2015. To Grow or Defend? Pine Seedlings Grow Less But Induce More Defences When a Key Resource is Limited. Tree Physiol. 35, 107–111.
Ferrenberg, S., Kane, J.M., Mitton, J.B., 2014. Resin Duct Characteristics Associated with Tree Resistance to Bark Beetles Across Lodgepole and Limber Pines. Oecologia 174, 1283–1292.
Franceschi, V.R., Krokene, P., Christiansen, E., Krekling, T., 2005. Anatomical and Chemical Defenses of Conifer Bark Against Bark Beetles and Other Pests. New Phytol. 167, 353–375.
Gaylord, M.L., Kolb, T.E., McDowell, N.G., 2015. Mechanisms of Piñon Pine Mortality after Severe Drought: A Retrospective Study of Mature Trees. Tree Physiol. 35, 806–816.
Gaylord, M.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yepez, E.A., Macalady, A.K., Pangle, R.E., McDowell, N.G., 2013. Drought Predisposes Pinon-Juniper Woodlands to Insect Attacks and Mortality. New Phytol. 198, 567–578.
Gaylord, M.L., Kolb, T.E., Wallin, K.F., Wagner, M.R., 2007. Seasonal Dynamics of Tree Growth, Physiology, and Resin Defenses in a Northern Arizona Ponderosa Pine Forest. Can. J. For. Res. 37, 1173–1183.
Geils, B.W., Hummer, K.E., Hunt, R.S., 2010. White Pines, Ribes, and Blister Rust: A Review and Synthesis. Forest Pathol. 40, 147–185.
Grissino-Mayer, H.D., 2001. Evaluating Crossdating Accuracy: A Manual and Tutorial for the Computer Program COFECHA. Tree-Ring Research 57, 205–221.
Hayes, J.L., Strom, B.L., 1994. 4-Allylanisole as an Inhibitor of Bark Beetle (Coleoptera: Scolytidae) Aggregation. J. Econ. Entomol. 87, 1586–1594.
Herms, D.A., Mattson, W.J., 1992. The Dilemma of Plants: To Grow or Defend. Q. Rev. Biol. 67, 283–335.
Hofstetter, R.W., Mahfouz, J.B., Klepzig, K.D., Ayres, M.P., 2005. Effects of Tree Phytochemistry on the Interactions among Endophloedic Fungi Associated with the Southern Pine Beetle. J. Chem. Ecol. 31, 539–560.
Holmes, R.L., Adams, R.K., Fritts, H.C., 1986. Tree-ring chronologies of Western North America: California, Eastern Oregon and Northern Great Basin; with: Procedures used in the chronology development work including users manuals for computer programs COFECHA and ARSTAN. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona.
Holtz, C.T., Schoettle, A.W., 2018. Is Resistance to Mountain Pine Beetle Associated with Genetic Resistance to White Pine Blister Rust in Limber Pine? Forests 9, 595.
Hood, S.M., Baker, S., Sala, A., 2016. Fortifying the Forest: Thinning and Burning Increase Resistance to a Bark Beetle Outbreak and Promote Forest Resilience. Ecol. Appl. 26, 1984–2000.
Hood, S.M., Sala, A., 2015. Ponderosa Pine Resin Defenses and Growth: Metrics Matter. Tree Physiol. 35, 1223–1235.
Hood, S.M., Sala, A., Heyerdahl, E.K., Boutin, M., 2015. Low-Severity Fire Increases Tree Defense Against Bark Beetle Attacks. Ecology 96, 1846–1855.
Howe, M., Keefover-Ring, K., Raffa, K.F., 2018. Pine Engravers Carry Bacterial Communities Whose Members Reduce Concentrations of Host Monoterpenes With Variable Degrees of Redundancy, Specificity, and Capability. Environ. Entomol. 47, 638–645.
Howe, M., Mason, C.J., Gratton, C., Keefover-Ring, K., Wallin, K., Yanchuk, A., Zhu, J., Raffa, K.F., 2020. Relationships Between Conifer Constitutive and Inducible Defenses Against Bark Beetles Change Across Levels of Biological and Ecological Scale. Oikos.
Huber, D.P.W., Gries, R., Borden, J.H., Pierce Jr., H.D., 2000. A Survey of Antennal Responses by Five Species of Coniferophagous Bark Beetles (Coleoptera: Scolytidae) to Bark Volatiles of Six Species of Angiosperm Trees. Chemoecology 10, 103–113.
Jamieson, M.A., Burkle, L.A., Manson, J.S., Runyon, J.B., Trowbridge, A.M., Zientek, J., 2017. Global Change Effects on Plant-Insect Interactions: The Role of Phytochemistry. Curr. Opin. Insect Sci. 23, 70–80.
Jones, K.L., Shegelski, V.A., Marculis, N.G., Wijerathna, A.N., Evenden, M.L., 2019. Factors Influencing Dispersal by Flight in Bark Beetles (Coleoptera: Curculionidae: Scolytinae): From Genes to Landscapes. Can. J. For. Res. 49, 1024–1041.
Joseph, G., Kelsey, R.G., Peck, R.W., Niwa, C.G., 2001. Response of Some Scolytids and their Predators to Ethanol and 4-allylanisole in Pine Forests of Central Oregon. J. Chem. Ecol. 27, 697–715.
Kane, J.M., Kolb, T.E., 2010. Importance of Resin Ducts in Reducing Ponderosa Pine Mortality from Bark Beetle Attack. Oecologia 164, 601–609.
Kane, J.M., Varner, J.M., Metz, M.R., van Mantgem, P.J., 2017. Characterizing Interactions Between Fire and Other Disturbances and Their Impacts on Tree Mortality in Western U.S. Forests. Forest Ecology and Management 405, 188–199.
Keane, R.E., Arno, S.F., 1993. Rapid Decline of Whitebark Pine in Western Montana: Evidence from 20-Year Remeasurements. West. J. Appl. For. 8, 44–47.
Keane, R.E., Gray, K.L., Dickinson, L.J., 2007. Whitebark pine diameter growth response to removal of competition. In: Agriculture, U.S.D.o., (Ed.) U.S. Forest Service, Rocky Mountain Research Station, pp. 1–9.
Keefover-Ring, K., Trowbridge, A., Mason, C.J., Raffa, K.F., 2016. Rapid Induction of Multiple Terpenoid Groups by Ponderosa Pine in Response to Bark Beetle-Associated Fungi. J. Chem. Ecol. 42, 1–12.
Keeling, C.I., 2016. Bark Beetle Research in the Postgenomic Era. In: Tittiger, C., Blomquist, G. (Eds.), Pine Bark Beetles - Advances in Insect Physiology. Simon Fraser University, Burnaby, BC, Canada, pp. 265–294.
Keeling, C.I., Bohlmann, J., 2006. Genes, Enzymes and Chemicals of Terpenoid Diversity in the Constitutive and Induced Defence of Conifers Against Insects and Pathogens. New Phytol. 170, 657–675.
Keen, R.M., Voelker, S.L., Bentz, B.J., Wang, S.-Y.-S., Ferrell, R., 2020. Stronger Influence of Growth Rate than Severity of Drought Stress on Mortality of Large Ponderosa Pines during the 2012–2015 California Drought. Oecologia 194, 359–370.
Kendall, K.C., Keane, R.E., 2000. The Decline of Whitebark Pine. In: Tomback, D.F., Arno, S.F., Keane, R.E. (Eds.), Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC, pp. 123–145.
Kenkel, N.C., Orlóci, L., 1986. Applying Metric and Nonmetric Multidimensional Scaling to Ecological Studies: Some New Results. Ecology 67, 919–928.
Kichas, N.E., Hood, S.M., Pederson, G.T., Everett, R.G., McWethy, D.B., 2020. Whitebark Pine (Pinus albicaulis) Growth and Defense in Response to Mountain Pine Beetle Outbreaks. For. Ecol. Manage. 457.
Kipfmueller, K.F., Swetnam, T.W., 2002. Climate and mountain pine beetle-induced tree mortality in the selway-bitterroot wilderness area. In: Resources, D.o.F., (Ed.) The University of Idaho, Moscow, ID, pp. 1–41.
Knapp, P.A., Soule, P.T., Maxwell, J.T., 2013. Mountain Pine Beetle Selectivity in Old-Growth Ponderosa Pine Forests, Montana, USA. Ecol. Evol. 3, 1141–1148.
LaMarche, V.C.J., Hirschboeck, K.K., 1984. Frost Rings in Trees as Records of Major Volcanic Eruptions. Nature 307, 121–126.
Langenheim, J.H., 1994. Higher Plant Terpenoids: A Phytocentric Overview of their Ecological Roles. J. Chem. Ecol. 20, 1223–1280.
Larocque, G.R., Luckai, N., Adhikary, S.N., Groot, A., Bell, F.W., Sharma, M., 2013. Competition Theory — Science and Application in Mixed Forest Stands: Review of Experimental and Modelling Methods and Suggestions for Future Research. Environmental Reviews 21, 71–84.
Lewinsohn, E., Gijzen, M., Croteau, R., 1991. Defense Mechanisms of Conifers. Plant Physiol. 96, 44–49.
Logan, J.A., Macfarlane, W.W., Willcox, L., 2010. Whitebark Pine Vulnerability to Climate-Driven Mountain Pine Beetle Disturbance in the Greater Yellowstone Ecosystem. Ecol. Appl. 20, 895–902.

Lotan, J.E., Critchfield, W.B., 1990. Pinus contorta Dougl. ex. Loud. - Lodgepole Pine. U. S.D.A Forest Service, Washington, D.C.
Mason, C.J., Keefover-Ring, K., Villari, C., Klutsch, J.G., Cook, S., Bonello, P., Erbilgin, N., Raffa, K.F., Townsend, P.A., 2019. Anatomical Defences against Bark Beetles Relate to Degree of Historical Exposure between Species and are Allocated Independently of Chemical Defences within Trees. Plant, Cell Environ. 42, 633–646.
Mattson, W.J., Haack, R.A., 1987. The Role of Drought in Outbreaks of Plant-Eating Insects. Bioscience 37, 110–118.
Meddens, A.J., Hicke, J.A., Ferguson, C.A., 2012. Spatiotemporal Patterns of Observed Bark Beetle-Caused Tree Mortality in British Columbia and the Western United States. Ecol. Appl. 22, 1876–1891.
Miller, D.R., Borden, J.H., 2000. Dose-Dependent and Species-Specific Responses of Pine Bark Beetles (Coeoptera: Scolytidae) to Monoterpenes in Association with Phermones. Can. Entomol. 132, 183–195.
Mizell 3rd, R.F., Frazier, J.L., Nebeker, T.E., 1984. Response of the Clerid Predator Thanasimus dubius (F.) to Bark Beetle Pheromones and Tree Volatiles in a Wind Tunnel. J. Chem. Ecol. 10, 177–187.
Moreira, X., Mooney, K.A., Rasmann, S., Petry, W.K., Carrillo-Gavilán, A., Zas, R., Sampedro, L., Novotny, V., 2014. Trade-Offs Between Constitutive and Induced Defences Drive Geographical and Climatic Clines in Pine Chemical Defences. Ecol. Lett. 17, 537–546.
Moreira, X., Sampedro, L., Zas, R., Pearse, I.S., 2016. Defensive Traits in Young Pine Trees Cluster into Two Divergent Syndromes Related to Early Growth Rate. PLoS ONE 11, e0152537.
Moreira, X., Zas, R., Solla, A., Sampedro, L., 2015. Differentiation of Persistent Anatomical Defensive Structures is Costly and Determined by Nutrient Availability and Genetic Growth-Defence Constraints. Tree Physiol. 35, 112–123.
Ormeno, E., Fernandez, C., Mevy, J.-P., 2007. Plant Coexistence Alters Terpene Emission and Content of Mediterranean Species. Phytochemistry 68, 840–852.
Perrakis, D.D.B., Agee, J.K., Eglitis, A., 2011. Effects of Prescribed Burning on Mortality and Resin Defenses in Old Growth Ponderosa Pine (Crater Lake, Oregon): Four Years of Post-Fire Monitoring. Natural Areas Journal 31, 14–25.
Phillips, M.A., Croteau, R.B., 1999. Resin-Based Defenses in Conifers. Trends in Plant Science - Reviews 4, 1360–1385.
Pitman, G.B., VitÉ, J.P., Kinzer, G.W., Fentiman, A.F., 1968. Bark Beetle Attractants: Trans-verbenol isolated from Dendroctonus. Nature 218, 168–169.
Powell, E.N., Raffa, K.F., 2011. Fire Injury Reduces Inducible Defenses of Lodgepole Pine against Mountain Pine Beetle. J. Chem. Ecol. 37, 1184–1192.
Prasifka, J.R., Spring, O., Conrad, J.r., Cook, L.W., Palmquist, D.E., Foley, M.E., 2015. Sesquiterpene lactone composition of wild and cultivated sunflowers and biological activity against an insect pest. J. Agric. Food Chem. 63, 4042–4049.
R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Raffa, K.F., 2014. Terpenes Tell Different Tales at Different Scales: Glimpses into the Chemical Ecology of Conifer - Bark Beetle - Microbial Interactions. J. Chem. Ecol. 40, 1–20.
Raffa, K.F., Aukema, B.H., Erbilgin, N., Klepzig, K.D., Wallin, K.F., 2005. Interactions Among Conifer Terpenoids and Bark Beetles Across Multiple Levels of Scale: An Attempt to Understand Links Between Population Patterns and Physiological Processes. In: Romeo, J.T. (Ed.), Chemical Ecology and Phytochemistry of Forest Ecosystems. Elsevier, pp. 79–118.
Raffa, K.F., Berryman, A.A., 1982. Accumulation of Monoterpenes and Associated Volatiles Following Inoculation of Grand Fir with a Fungus Transmitted by the Fir Engraver, Scolytus Ventralis (Coleoptera: Scolytidae). Can. Entomol. 114, 797–810.
Raffa, K.F., Mason, C.J., Bonello, P., Cook, S., Erbilgin, N., Keefover-Ring, K., Klutsch, J. G., Villari, C., Townsend, P.A., 2017. Defence Syndromes In Lodgepole - Whitebark Pine Ecosystems Relate To Degree Of Historical Exposure To Mountain Pine Beetles. Plant, Cell Environ. 40, 1791–1806.
Raffa, K.F., Powell, E.N., Townsend, P.A., 2013. Temperature-Driven Range Expansion of an Irruptive Insect Heightened by Weakly Coevolved Plant Defenses. Proc. Natl. Acad. Sci. 110, 2193–2198.
Reed, C.C., Ballantyne, A.P., Cooper, L.A., Sala, A., 2018. Limited Evidence for CO2-Related Growth Enhancement in Northern Rocky Mountain Lodgepole Pine Populations Across Climate Gradients. Glob. Change Biol.
Reed, C.C., Hood, S.M., 2020. Few Generalizable Patterns of Tree-Level Mortality During Extreme Drought and Concurrent Bark Beetle Outbreaks. Sci. Total Environ. 750, 141306.
Reid, M.L., Sekhon, J.K., LaFramboise, L.M., 2017. Toxicity of Monoterpene Structure, Diversity and Concentration to Mountain Pine Beetles, Dendroctonus ponderosae: Beetle Traits Matter More. J. Chem. Ecol. 43, 351–361.
Reineke, L.H., 1933. Perfecting a Stand-Density Index for Even-Aged Forests. Journal of Agricultural Research 46, 627–638.
Roy, B.A., Alexander, H.M., Davidson, J., Campbell, F.T., Burdon, J.J., Sniezko, R., Brasier, C., 2014. Increasing Forest Loss Worldwide from Invasive Pests Requires New Trade Regulations. Front. Ecol. Environ. 12, 457–465.
Samman, S., Schwandt, J.W., Wilson, J.L., 2003. Managing for healthy white pine ecosystems in the United States to reduce the impacts of white pine blister rust. In: Agriculture, U.S.D.o., (Ed.), Forest Service, Missoula, Montana, pp. 10.
Schwandt, J.W., Lockman, I.B., Kliejunas, J.T., Muir, J.A., 2010. Current Health Issues and Management Strategies for White Pines in the Western United States and Canada. Forest Pathol. 40, 226–250.
Seybold, S.J., Huber, D.P.W., Lee, J.C., Graves, A.D., Bohlmann, J., 2006. Pine Monoterpenes and Pine Bark Beetles: A Marriage of Convenience for Defense and Chemical Communication. Phytochem. Rev. 5, 143–178.
Shanahan, E., Irvine, K.M., Thoma, D., Wilmoth, S., Ray, A., Legg, K., Shovic, H., 2016. Whitebark Pine Mortality Related to White Pine Blister Rust, Mountain Pine Beetle Outbreak, and Water Availability. Ecosphere 7.
Slack, A.W., Kane, J.M., Knapp, E.E., Sherriff, R.L., 2017. Contrasting Impacts of Climate and Competition on Large Sugar Pine Growth and Defense in a Fire-Excluded Forest of the Central Sierra Nevada. Forests 8, 244.
Slack, A.W., Zeibig-Kichas, N.E., Kane, J.M., Varner, J.M., 2016. Contingent Resistance in Longleaf Pine (Pinus palustris) Growth and Defense 10 Years Following Smoldering Fires. For. Ecol. Manage. 364, 130–138.
Smith, R.H., 2000. Xylem Monoterpenes of Pines: Distribution, Variation, Genetics, Function. In: Service, U.S.D.A.F. (Ed.), Pacific Southwest Research Station. Albany, California, pp. 1–454.
Sparks, A.M., Smith, A.M.S., Talhelm, A.F., Kolden, C.A., Yedinak, K.M., Johnson, D.M., 2017. Impacts of Fire Radiative Flux on Mature Pinus ponderosa Growth and Vulnerability to Secondary Mortality Agents. International Journal of Wildland Fire 26.
Stokes, M.A., Smiley, T.L., 1996. An Introduction to Tree-Ring Dating. The University of Arizona Press, Tucson, AZ.
Tepley, A.J., Hood, S.M., Keyes, C.R., Sala, A., 2020. Forest Restoration Treatments in a Ponderosa Pine Forest Enhance Physiological Activity and Growth Under Climatic Stress. Ecological. Applications.
Tomback, D.F., Achuff, P., 2010. Blister Rust and Western Forest Biodiversity: Ecology, Values and Outlook for White Pines. Forest Pathol. 40, 186–225.
Tomback, D.F., Blakeslee, S.C., Wagner, A.C., Wunder, M.B., Resler, L.M., Pyatt, J.C., Diaz, S., 2016a. Whitebark Pine Facilitation at Treeline: Potential Interactions for Disruption by an Invasive Pathogen. Ecol. Evol. 6, 5144–5157.
Tomback, D.F., Resler, L.M., Keane, R.E., Pansing, E.R., Andrade, A.J., Wagner, A.C., 2016b. Community Structure, Biodiversity, and Ecosystem Services in Treeline Whitebark Pine Communities: Potential Impacts from a Non-Native Pathogen. Forests 7, 21.
Trapp, S., Croteau, R., 2001. Defensive Resin Biosynthesis in Conifers. Annual Review of Plant Physiology and Plant Molecular Biology 52, 689–724.
Trowbridge, A.M., 2014. Evolutionary Ecology of Chemically Mediated Plant-Insect Interactions. Ecology and the Environment, pp. 143–176.
Trowbridge, A.M., Bowers, M.D., Monson, R.K., 2016. Conifer Monoterpene Chemistry During an Outbreak Enhances Consumption and Immune Response of an Eruptive Folivore. J. Chem. Ecol. 42, 1281–1292.
Trowbridge, A.M., Stoy, P.C., Adams, H.D., Law, D.J., Breshears, D.D., Helmig, D., Monson, R.K., 2019. Drought Supersedes Warming in Determining Volatile and Tissue Defenses of Piñon Pine (Pinus edulis). Environ. Res. Lett. 14.
Valor, T., Ormeno, E., Casals, P., 2017. Temporal Effects of Prescribed Burning on Terpene Production in Mediterranean Pines. Tree Physiol. 37, 1622–1636.
van de Gevel, S., Larson, E., Grissino-Mayer, H., 2017. Separating Trends in Whitebark Pine Radial Growth Related to Climate and Mountain Pine Beetle Outbreaks in the Northern Rocky Mountains, USA. Forests 8, 195.
van Mantgem, P.J., Stephenson, N.L., 2007. Apparent Climatically Induced Increase of Tree Mortality Rates in a Temperate Forest. Ecol. Lett. 10, 909–916.
van Mantgem, P.J., Stephenson, N.L., Keifer, M., Keeley, J., 2004. Effects of an Introduced Pathogen and Fire Exclusion on the Demography of Sugar Pine. Ecol. Appl. 14, 1590–1602.
Vázquez-González, C., Zas, R., Erbilgin, N., Ferrenberg, S., Rozas, V., Sampedro, L., 2020. Resin Ducts as Resistance Traits in Conifers: Linking Dendrochronology and Resin-Based Defenses. Tree Physiol.
Consulting, Voortech, 2005. The Tree Ring Measuring Program Project J2X. Voortech Consulting.
Wagner, A., Tomback, D., Resler, L., Pansing, E., 2018. Whitebark Pine Prevalence and Ecological Function in Treeline Communities of the Greater Yellowstone Ecosystem, U.S.A.: Potential Disruption by White Pine Blister Rust. Forests 9 (635).
Waring, R.H., Pitman, G.B., 1985. Modifying Lodgepole Pine Stands to Change Susceptibility to Mountain Pine Beetle Attack. Ecology 66, 889–897.
Williams, H., Hood, S., Keyes, C., Egan, J., Negrón, J., 2018. Subwatershed-Level Lodgepole Pine Attributes Associated with a Mountain Pine Beetle Outbreak. Forests 9.
Yi, M., Jia, T., Dong, L., Zhang, L., Leng, C., Liu, S., Lai, M., 2021. Resin Yield in Pinus elliottii Engelm. is Related to the Resin Flow Rate, Resin Components and Resin Duct Characteristics at Three Locations in Southern China. Ind. Crops Prod. 160.
Zas, R., Moreira, X., Ramos, M., Lima, M.R.M., Nunes da Silva, M., Solla, A., Vasconcelos, M.W., Sampedro, L., 2014. Intraspecific Variation of Anatomical and Chemical Defensive Traits in Maritime Pine (Pinus pinaster) as Factors in Susceptibility to the Pinewood Nematode (Bursaphelenchus xylophilus). Trees 29, 663–673.
Zhang, C.-Y., Luo, L., Xia, J., Song, Y.-N., Zhang, L.-J., Zhang, M., Rahman, K., Ye, Y., Zhang, H., Zhu, J.-Y., 2018. Sesquiterpenes and Lignans from the Flower Buds of Daphne genkwa and their Nitric Oxide Inhibitory Activities. Nat. Prod. Res. 32, 2893–2899.
Zhang, Y., Li, Z.-X., Yu, X.-D., Fan, J., Pickett, J.A., Jones, H.D., Zhou, J.-J., Birkett, M.A., Caulfield, J., Napier, J.A., Zhao, G.-Y., Cheng, X.-G., Shi, Y., Bruce, T.J., Xia, L.-Q., 2015. Molecular Characterization of Two Isoforms of a Farnesyl Pyrophosphate Synthase Gene in Wheat and their Roles in Sesquiterpene Synthesis and Inducible Defence against Aphid Infestation. New Phytol. 206, 1101–1115.
Zhao, M., Zhang, N., Gao, T., Jin, J., Jing, T., Wang, J., Wu, Y., Wan, X., Schwab, W., Song, C., 2020. Sesquiterpene Glucosylation Mediated by Glucosyltransferase UGT91Q2 is Involved in the Modulation of Cold Stress Tolerance in Tea Plants. New Phytol. 226, 362–372.

Zhao, S., Erbilgin, N., 2019. Larger Resin Ducts Are Linked to the Survival of Lodgepole Pine Trees During Mountain Pine Beetle Outbreak. Front. Plant Sci. 10, 1459.
Zhao, S., Klutsch, J.G., Cale, J.A., Erbilgin, N., 2019. Mountain Pine Beetle Outbreak Enhanced Resin Duct-Defenses of Lodgepole Pine Trees. For. Ecol. Manage. 441, 271–279.
Zhao, Y., Zhou, Y., Jiang, H., Li, X., Gan, D., Peng, X., Zhu, S., Cheng, B., 2011. Systematic Analysis of Sequences and Expression Patterns of Drought-Responsive Members of the HD-Zip Gene Family in Maize. PLoS ONE 6, e28488.