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Whitebark pine (*Pinus albicaulis*) growth and defense in response to mountain pine beetle outbreaks

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ABSTRACT

Whitebark pine (*Pinus albicaulis*) is a critical forest species of Northern Rocky Mountain upper subalpine ecosystems, yet little is known about the physiological response of whitebark pine to disturbance (e.g. fire, bark beetles, and pathogens) across a range of diverse environmental gradients. Resin-based defenses have long been recognized as the primary mechanism by which conifers respond to attack by bark beetles and pathogens and several studies have linked resin duct properties to survivorship during periods of increased beetle activity. However, to our knowledge, no studies have compared axial resin ducts in the secondary xylem of whitebark pine across pairs of living and dead whitebark pine trees to better understand survivorship following multiple disturbances including mountain pine beetle and white pine blister rust. We found a clear distinction in growth and defense characteristics between live and dead whitebark pine. Across our study sites on the Flathead Indian Reservation in northwestern Montana, live whitebark pine produced larger resin ducts with a greater annual investment in resin-based defenses than whitebark pine that died. Resin duct size, duct area, and relative duct area were all greater in live whitebark pine (by 56%, 48%, and 57%, respectively) and these were the most important variables influencing whitebark pine survivorship. In contrast, whitebark pine that had died grew faster over time (22% larger ring widths) than their live counterparts and also produced more resin duct structures (20% more ducts on average). Whitebark pine at our study sites exhibit differing strategies in the allocation of resources toward growth and defense, with the majority of survivors of recent disturbance investing more in defensive structures than growth. Our results support the idea that maintaining genetic variability and the associated suite of differing physiological traits promotes diverse response strategies to a complex array of biophysical and biological stressors that might leave a species vulnerable to extinction across its range.

1. Introduction

Whitebark pine (*Pinus albicaulis*) is a critical forest species of U.S. Northern Rocky Mountain subalpine ecosystems (Arno and Hoff, 1989, Keane, 2000, Tomback et al., 2001). Often dominating treeline, whitebark pine is considered a keystone species, with high cultural and ecological significance (Cole, 1990, Mills and Doak, 1993, Tomback et al., 2001). Whitebark pine is one of the few species that thrives at high altitudes (> 2000 masl) where they stabilize erosive slopes; promote snow accumulation; increase snowpack retention and effectively modulate moisture loss in subalpine regions, influencing water availability at lower elevations (Arno and Hoff, 1989, Tomback and Kendall, 2001, Bockino and Tinker, 2012). Whitebark pine seeds are highly nutritious and an important food source for several species of wildlife, including grizzly bears (*Ursus arctos horribilis*), black bears (*U. americanus*), and a number of small mammals and birds. Seeds are predominately dispersed by the Clark's nutcracker (*Nucifraga Columbiana*), often cached in disturbed areas, such as recently burned landscapes, where, if forgotten, the cached seeds germinate to become the whitebark pine forests of tomorrow. Whitebark pine is an important pioneer species, as the hearty seedlings colonize areas and ameliorate site conditions, promoting additional vegetative growth through tree island initiation (Tomback et al., 1993, Tomback et al., 2016). 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 white pine blister rust (*Cronartium ribicola*). These stressors, primarily blister rust, have already decimated populations (by as much as 90%) in some areas of the Northern Rocky Mountains (Keane and Arno, 1993, Kendall and Keane, 2000, Macfarlane et al., 2013, Shanahan et al., 2016, Amberson et al., 2018).

While insects, fire, disease, and secondary effects of drought (including increased tree stress and predisposition to these disturbances) have contributed to recent mortality of whitebark pine, these processes also play an important role in the long-term establishment and persistence of Northern Rocky Mountain whitebark pine forests. However, historical records detailing the relationship between disturbance and whitebark pine ecosystem dynamics are particularly lacking. For example, a metanalysis of paleoecological data suggest that the abundance of *Pinus* subgenus *strobus*, as inferred from pollen percentages, was greater (particularly at lower elevations) during the Holocene

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summer insolation maximum (~9 k.y.a.) when summer temperatures were warmer, bark beetle activity was prevalent, and fire activity was high in the Western U.S. (Iglesias et al., 2015). This research suggests a possible complex interaction between temperature, fire, and the insect dynamics that has developed over thousands of years and the need to better understand how five needle pines (*P. strobus* subgenus) have persisted in the past and will respond to multiple disturbances in the future. Research is needed to better understand the physiological response of whitebark pine to fire frequency and severity and beetle outbreaks across a range of diverse environmental gradients. This is especially true given that current species risk assessments for whitebark pine rely on bioclimatic models that include little information on disturbance processes and physiological adaptability of whitebark pine to interactions and feedbacks between changing climatic and disturbance regimes.

Better understanding how physiological characteristics of whitebark pine (specifically the allocation of resources to growth and defense) influence survival following the cumulative effects of fire, bark beetles, and white pine blister rust would provide critical information to resource managers tasked with managing this keystone species. Across all species of pine, research shows that during beetle attacks, even at peak epidemic levels, there are mature individuals that remain uncolonized by beetles, and that these resistant individuals may have different defense traits (Strom et al., 2002, Hood et al., 2016). For example, Strom et al. (2002) found oleoresin flow from progeny of mature loblolly pines (*P. taeda*) that “escaped” mortality during an outbreak of southern pine beetle (*Dendroctonus frontalis*) was higher compared to the general population. Similarly, several studies have established the importance of resin ducts as defense traits in ponderosa pine (*P. ponderosae*) and piñon pine (*P. edulis*) (Kane and Kolb, 2010, Gaylord et al., 2013, Hood et al., 2016). Survivorship of individuals within such diverse populations suggests an intrinsic level of resistance that can be genetically passed on to the survivors’ progeny (de la Mata et al., 2017, Six et al., 2018). This is supported by research that shows that the capacity to produce defensive features (such as resin ducts) and the composition of chemical defenses (e.g. chemotypes) are under strong genetic control, resulting from site-specific selective pressures that moderate growth and defense relationships over time, although there is considerable variability in this response within and across species (Hannrup et al., 2004, Rosner and Hannrup, 2004, Moreira et al., 2014, Moreira et al., 2015, Westbrook et al., 2015, Moreira et al., 2016).

Within conifers, resin-based defenses have long been recognized as the primary mechanism by which trees respond to attack by bark beetles and pathogens (Langenheim, 1994, Phillips and Croteau, 1999, Trapp and Croteau, 2001, Franceschi et al., 2005, Keeling and Bohlmann, 2006). Resin ducts are permanent anatomical features within the secondary xylem and have been shown to correspond with resin flow, such that greater total area of resin ducts facilitates increased production, storage, and mobilization of oleoresin to sites of wounding (Hood and Sala, 2015). As resin ducts are produced regularly (typically every year to every few years), they can be measured, in conjunction with tree rings, to assess resource allocation to growth and defense over time. Several researchers have linked physical properties of resin ducts to survivorship during periods of increased beetle activity (Kane and Kolb, 2010, Ferrenberg et al., 2014, Hood and Sala, 2015, Hood et al., 2015, Hood et al., 2016). For instance, in conifer forests of northern Arizona, Kane and Kolb (2010) found that ponderosa pine that persisted through drought and stand-level bark beetle activity produced more resin ducts with a greater overall duct density and relative duct area than trees that were killed. Ferrenberg et al. (2014) found that lodgepole and limber pines in Colorado both produced more resin ducts over the most recent ten years of growth compared to trees that died during a bark beetle outbreak, while Hood et al. (2015) found that ponderosa pine that survived beetle attacks in Montana produced larger resin ducts with a greater relative area.

Drought and wildfire are also thought to influence the development of defensive traits. For example, fire has been shown to have a measurable impact on the formation of resin ducts and oleoresin and may potentially influence resin chemistry by altering nutrient availability (Cannac et al., 2009, Perrakis et al., 2011, Powell and Raffa, 2011, Hood et al., 2015, Hood et al., 2016). Further, under drought scenarios, increased stomatal closure can reduce carbon assimilation, which can reduce resource availability for the production of resin ducts and chemical compounds, which may predispose trees to insects and pathogens (Gaylord et al., 2007, Six and Adams, 2007, Sala et al., 2010, Gaylord et al., 2013). While fewer studies have investigated the impacts of drought on resin duct characteristics, Gaylord et al. (2013) found that an experimental three-year drought reduced both the size and density of resin ducts in piñon pine. Wimmer and Grabner (1997) found that Norway spruce (*Picea abies*) resin duct density increased during periods of above-average temperatures while production decreased during periods of above-average precipitation. This highlights complex relationships between physiological processes and the influence of climate that is poorly explored for many tree species.

While physical and chemical defenses are critical for mediating plant-herbivore-pathogen interactions, the production and proliferation of defensive structures and chemical compounds is energetically expensive with high demand for relatively limited carbon resources (Lewinsohn et al., 1991, Stamp, 2003, Moreira et al., 2014, Trowbridge, 2014). Given adequate resource availability, research suggests trees will preferentially allocate resources toward primary production, including diameter and height growth as well as development of leaves, cones, and roots (Trowbridge, 2014, Jamieson et al., 2017). However, in processes that are less well understood, trees simultaneously utilize carbon reserves in the production of defensive features (e.g. resin ducts) and secondary metabolites (e.g. terpenoids, alkaloids, and phenols) to protect crucial tissues from damage by herbivory and pathogens (Trowbridge, 2014, Jamieson et al., 2017). The divergent allocation of resources towards biophysical processes moderating growth and defense has long been thought to reflect an important tradeoff in plant physiology and many hypotheses have been proposed to explain different patterns observed in nature and laboratory experiments (Herms and Mattson, 1992, Stamp, 2003, Endara and Coley, 2011, Trowbridge, 2014).

Central to these hypotheses is the broader idea that resource allocation towards defense enhances plant fitness and that inter- and intra-specific variability can be explained by tradeoffs between growth and defense, whereby external factors including resource availability, abiotic stress, and pathogen/herbivore pressures all influence investment in defensive systems (Moreira et al., 2014, Trowbridge, 2014, Ferrenberg et al., 2015, Jamieson et al., 2017). Numerous studies looking to establish evidence for specific hypotheses have found that they are not mutually exclusive and that the allocation of resources to growth and defense depends on specific species and environmental conditions (climate, topography, intra- and inter-specific competition, trait heritability, and disturbance legacies) (Stamp, 2003, Trowbridge, 2014, Mason et al., 2019).

Currently, evaluation of growth and defense tradeoffs has focused on relatively few species of limited size and age classes (Rosner and Hannrup, 2004, Ferrenberg et al., 2015). To our knowledge, only one other study (Mason et al., 2019) has considered such tradeoffs for mature whitebark pine in natural settings and no studies have compared axial resin ducts in the secondary xylem of whitebark pine across pairs of living trees and trees that were killed by varying combinations of mountain pine beetle (*D. ponderosae*) and white pine blister rust. In this study, we evaluated whether diameter growth and structural characteristics of resin ducts differed between live and dead whitebark pine trees and whether trees that lived (hereafter “live trees”) and trees that died (hereafter “dead trees”) responded similarly to climate. We hypothesized that: H1) live whitebark pines would exhibit greater and more sustained growth than dead whitebark pines during the overlap of their lifespan, and H2) currently live whitebark pines would have increased resin duct defenses, specifically, increased resin duct size, number, and cumulative area than whitebark pines that were killed by disturbance. We anticipated that surviving individuals would have more robust constitutive defenses and that there would be a detectable difference in growth and defense anatomy compared to individuals that have died. We also investigated whether seasonal climate had any influence on whitebark pine growth and defense, as other research has shown strong influence of multiple disturbance interactions (e.g., drought and beetle attacks) acting on survivorship (Gaylord et al., 2013, Gaylord et al., 2015).

Our hypotheses are based on previous research which suggests that vigorous trees (those with increased growth and thus increased photosynthetic capacity) can fix comparatively more carbon and are thus able to allocate a greater 'surplus' of carbon annually to the development of physical and chemical defenses (Ferrenberg et al., 2014, Hood and Sala, 2015, Hood et al., 2016). However, not all research supports a correlation between greater growth rates and increased defensive capacity in trees. For example, several studies suggest an opposite strategy, whereby trees growing in resource-rich environments may invest less in constitutive defenses (such as axial resin ducts) relative to growth. It is argued that trees adopting this strategy rely more on inducible defenses, which are synthesized *de novo* in response to attack or injury and may thus allocate more annual carbon towards primary production at the expense of defense (Ferrenberg et al., 2014, Moreira et al., 2014, Moreira et al., 2015). These seemingly conflicting results suggest that growth and defense strategies employed by trees are complex and species specific, likely varying across habitat and ontogeny. Thus, more research is needed to investigate these relationships across a range of species and habitats.

The lack of empirical studies evaluating growth and defense theory for high elevation pines that experience multiple, complex disturbance stressors, highlights a need to better understand growth and defense characteristics across a range of biophysical gradients. Understanding resin defense systems is of particular importance in this regard as these advanced biochemical structures represent the primary defense mechanism of whitebark pine to biotic disturbance. Evaluating relationships between resin duct structures and oleoresin production and disturbance can provide valuable insight into overall defensibility of these trees to stressors that are projected to increasingly impact this important cultural and ecological species.

2. Methods

2.1. Site description

Data for this study were collected on two high-elevation whitebark pine sites on the Flathead Indian Reservation during the summer of 2016 as part of a larger fire history reconstruction for the Confederated Salish and Kootenai Tribes (CSKT; Fig. 1). We selected sites where whitebark pine was an important component of the canopy (> 15% canopy cover). Canopy species at both sites consist of lodgepole pine (*P. contorta* var *latifolia*) and whitebark pine, with smaller components of subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Herbaceous cover across both sites consists primarily of grouse whortleberry (*Vaccinium scoparium*), common huckleberry (*V. membranaceum*), dwarf huckleberry (*V. cespitosum*), bear grass (*Xerophyllum tenax*), and smooth woodrush (*Luzula hitchcockii*). Menziesia (*Menziesia ferruginea*) was also a sizable understory component at the Boulder site (BLD) but was not found at the Three Lakes Peak site (3LK). Evidence of disturbance legacies, including wildfires, insect and pathogen outbreaks were common at both sites.

The 3LK site is located in the Reservation Divide Mountains between the Flathead Indian Reservation and Missoula, Montana. Mean annual temperatures at this location are generally cool, ranging from 2° to 5° C with a 30- to 60-day frost-free period. Precipitation averages 1143 mm per year, which occurs primarily as snowfall from November through March. Soils at this site are from the Phillcher series and Halloway-Waldbillig series and consist of gravelly ashy silt loams that are moderately drained. Whitebark pine is a notable tree component at 3LK, comprising 15% of all sampled individuals (225 out of 1507 trees). 3LK is characterized by complex disturbance legacies, with evidence for mixed- and low-severity fire regimes on southern and eastern aspects and lethal fire regimes on northern and western aspects. The area has also been affected by numerous large-scale bark beetle outbreaks, occurring in the 1930s, 1960s–1980s and most recently 2002–2009 (Arno and Hoff, 1989, Kipfmueller and Swetnam, 2002, Buotte et al., 2017, van de Gevel et al., 2017). The majority of whitebark pine mortality at this location was due to cumulative impacts from mountain pine beetle and white pine blister rust, which was introduced to this region of the Northern Rocky Mountains circa 1950 (Mielke, 1943, Samman et al., 2003, Geils et al., 2010). Of the 225 sampled whitebark pine trees, 73% were dead, with the majority of dead trees (88%) showing evidence of beetle activity (*J*-shaped galleries along the tree stem and/or presence of blue-stain fungi (*Grosmannia clavigera*), which is vectored by bark beetles during colonization.

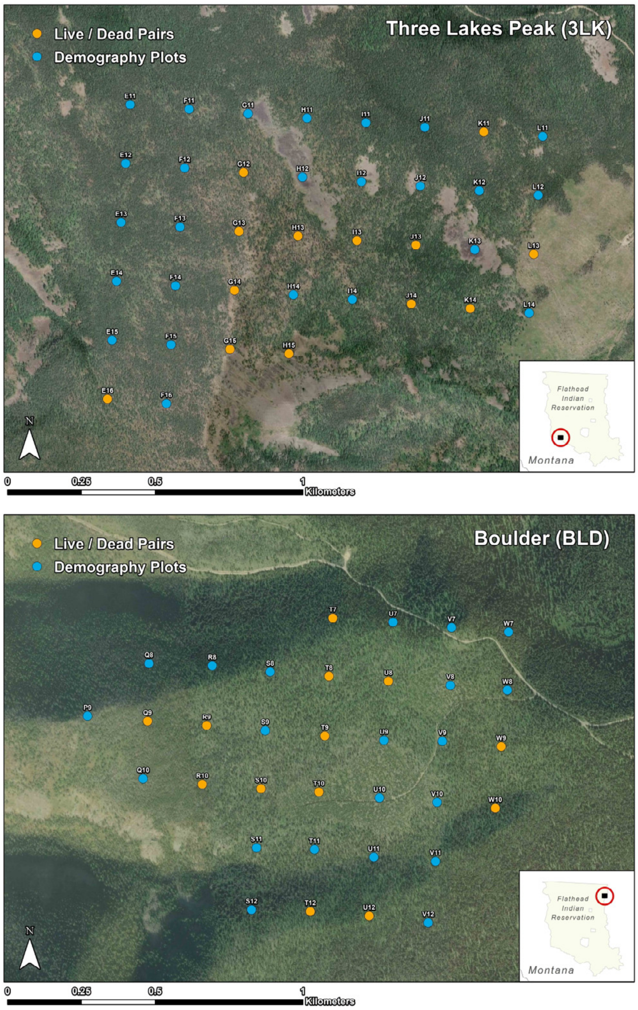

Fig. 1. Three Lakes Peak (top) and Boulder (bottom) study sites on the Flathead Indian Reservation in northwestern Montana. Permanent plots ("Demography Plots") were located on a 200 m grid as part of a fire history study for the Reservation. Plots cover approximately 100 ha at 3LK and 88 ha at BLD. Orange plots (covering approximately 24 ha at each site) had suitable pairs of live/dead whitebark pine trees (those that were closer than 20 m and less than 3 cm difference in DBH). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The BLD site is located approximately 74 km away in the Western

Mission Mountains on the Eastern side of Flathead Lake. Mean annual temperatures for this site are similar to 3LK, with average temperatures ranging from 1 to 6 °C with a 20- to 70-day frost-free period. This area receives slightly more precipitation than 3LK, with an average of 1397 mm annually, which occurs primarily as snowfall from November through March. Soils at this site are of the Halloway series and consist of gravelly silt loam that are also moderately drained. Whitebark pine was more prominent at this site, comprising 36% of all sampled individuals (476 out of 1320 trees). Of these, 14% were live and 86% were dead, the majority of which (71%) had evidence of bark beetle activity. This area is characterized largely by mixed- and lethal-severity fire regimes and had a similar recent history of 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). White pine blister rust was also evident at this site but was not as extensive as at 3LK (unpub data).

2.2. *Field sampling methods*

A 200 m grid was overlain across each site using a combination of remote sensing and field surveying for optimal placement (Fig. 1). The sample grid was selected across whitebark pine stands ranging from low- to high-severity fire regimes. This gridded sampling design effectively captured much of the topographic and vegetative variability at each of the sites, providing for a more 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 along cardinal directions, with a total of 38 plots for the 3LK site (covering approximately 100 ha) and 34 plots for the BLD site (covering approximately 88 ha; Fig. 1).

Each macroplot was spatially referenced with Garmin Rhino 650 GPS units 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. 2). 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), size (DBH), canopy base height, crown class (dominant, codominant, intermediate, or suppressed), tree height, 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 (5.6 m diameter) was also established around plot center, where all understory vegetation was identified and estimates made for percent cover of all species (Fig. 2).

2.3. *Live/dead tree pairing*

To assess the influence of disturbance on whitebark pine physiology (growth and defense characteristics) live trees and corresponding dead trees (hereafter “pairs”) were identified from the macroplot data. Suitable pairs were identified based on distance ($<$ 20 m apart) and size ($<$ 3 cm difference DBH) to control for potential microsite differences (Kane and Kolb, 2010, Hood and Sala, 2015). As a result of these pairing criteria, only a subset of the macroplots contained suitable pairs for this analysis (Fig. 1). Overall, 30 pairs were identified at the 3LK site across 13 macroplots and 42 pairs were identified at the BLD site across 13 macroplots for a total of 144 sampled trees (72 live and 72 dead; Fig. 1). It is important to note that our live trees did not exhibit any signs of active bark beetle attack (such as pitch-tubes and canopy dieback), so our investigation of resin duct characteristics between live and dead whitebark pine trees relates to host-selection, rather than a post-selection response in live trees.

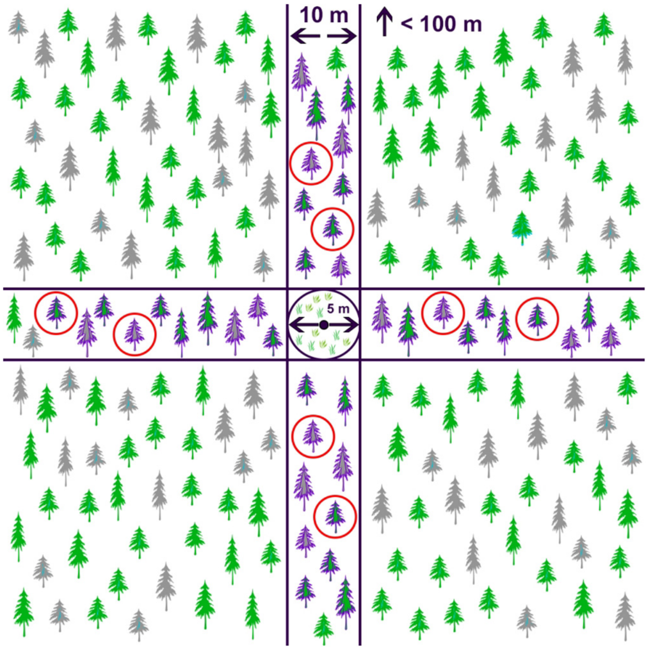

Fig. 2. Conceptual diagram of the plot sampling protocol. From plot center, four 10 m wide belt transects were extended in each cardinal direction and the closest 10 trees ($>$ 15 cm DBH) in each transect were sampled (to a maximum distance of 100 m). A 5.6 m diameter plot was established around plot center to measure herbaceous vegetation. Coloring: Live trees (green); dead trees (grey); sampled trees for fire history study (purple highlighting); live/dead pairs of whitebark pine trees (red circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. *Sample preparation*

Increment cores were air-dried and processed using standard dendrochronological techniques (Holmes et al., 1986, Cook and Kairiukstis, 1990, Stokes and Smiley, 1996). All 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 crossdated visually and graphically using ring-width patterns and frost rings (LaMarche and Hirschboeck, 1984). Crossdating was facilitated by developing site-specific chronologies from ring-width measurements, which were 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 in the resulting image 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 measurements across five categories, including non-relativized defense 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}), as well as resin duct measures that have been relativized to ring area, including duct density (number of resin ducts mm^{-2} year^{-1}) and relative duct area (% annual ring) (Kane and Kolb, 2010, Hood and Sala, 2015, Hood et al., 2016).

2.5. *Data analysis*

To assess possible tradeoffs in the allocation of carbon towards growth and defense we evaluated relationships between resin duct metrics and radial growth for live and dead trees (Kane and Kolb, 2010,

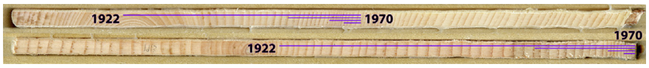

Fig. 3. Example of increment cores from a pair of live (top) and dead (bottom) whitebark pine. Trees were paired based on distance (< 20 m) and size (< 3 cm difference in diameter at breast height). Growth and defense measures were compared across all overlapping years, as well as 20-, 10-, and 5-year periods (series of progressively shorter purple lines in the figure). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Ferrenberg et al., 2014, Hood and Sala, 2015). Following the methods of (Kane and Kolb, 2010), we calculated growth and defense metrics annually (for all overlapping years between live and dead trees), as well as in 20-, 10-, and 5-year periods corresponding to the 20-, 10-, and 5-year windows prior to mortality (Fig. 3). For growth measures, we utilized ring area (ring width * core diameter) as well as a standardized, unitless ring width index (RWI). The RWI was developed through interactive detrending in the dplR package (version 1.64) (Bunn, 2008) in R (version 3.31) (R_Development_Core_Team, 2008). 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% 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 and Peters, 1997). Conservative detrending options were selected 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. For the majority of ring width series (87%) a negative exponential fit was selected, while a spline model was selected for 13% of the records. We chose to use RWI over basal area increment (BAI) because the assumptions of BAI are not well-suited for growth dynamics of high-elevation whitebark pine stands. For instance, some of the sampled whitebark pine were multi-stemmed trees with fused trunks (a common feature due to whitebark pine seed caching). The sampled stems had small DBH values, but ring width series from the collected increment cores reflected growth in a larger portion of the stem than we were able to measure (as we retrieved increment cores near the root collar), producing unrealistic BAI values (Maher et al., 2018).

We used Wilcoxon's paired *t*-tests to assess differences in growth and defense between pairs of live and dead whitebark pine at each site (Kane and Kolb, 2010) and applied a Bonferroni correction factor ($\alpha = 0.05/4 = 0.0125$) for all growth periods to account for multiple comparisons across similar growth periods (e.g. mean growth for total, 20-, 10- and 5-year time periods). We utilized a combination of multivariate analyses of variance, correlation analyses and regression analyses to examine relationships between annual radial growth (ring area and growth index) and defense metrics (resin duct size, production, area, density and relative area).

Next, we investigated the degree to which climate modulated growth and defense in whitebark pine and whether there were detectable differences in the response of live and dead trees to seasonal changes in climate. Estimates of local climate within the study areas were obtained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM), as instrumental weather data were not available at these sites (Daly et al., 1994, Kipfmueller and Salzer, 2010, Abatzoglou et al., 2017). PRISM data were obtained at a spatial resolution of 4 km using the AN 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 areas with complex topography (Millar et al., 2007, Kipfmueller and Salzer, 2010, Guiterman et al., 2015, Hood et al., 2015, Carnwath and Nelson, 2016, Ferrenberg et al., 2017, Slack et al., 2017, Cansler et al., 2018, Goeking and Izlar, 2018). Using the treeclim package in R (version 2.0) (Zang and Biondi, 2015) we developed 30-year moving correlation windows over two year time-step intervals to assess the influence climate on growth and defense metrics for live and dead trees. We grouped monthly climate data into seasonal windows to evaluate the more nuanced response of trees to seasonal variability. For instance, "*winter*" encompasses December (from the previous year) through March, while "*spring*" includes April and May, and "*summer*" is defined as June through August. Monthly climate variables obtained for this analysis included average temperature, precipitation, and the Palmer Drought Severity z-Index (z-PDSI; a measure of meteorological drought). Positive values in the z-PDSI correspond to wet (non-drought) conditions while negative values translate to drier (drought) periods. The z-PDSI metric contains no built-in autocorrelation to carry moisture from season to season. Consequently, this drought metric responds nearly instantaneously to precipitation (or lack thereof), making season-to-season moisture differences discernable, and better representing short-term and shallow soil moisture conditions (Abatzoglou et al., 2017). We opted to use z-PDSI as we were interested in how meteorological drought might influence whitebark pine growth and resin duct development. z-PDSI data were acquired using the WestWide Drought Tracker for the western Montana climate division (Abatzoglou et al., 2017).

We assessed the strength of correlations between growth and defense metrics and climate variables across the full record (1911–2004) as well as across two time intervals: early 20th century (1911–1960) and late 20th century (1961–2004). We hypothesized that increased bark beetle activity post-1960 coupled with the introduction of blister rust to the Flathead Indian Reservation around 1950 may have acted in concert with climatic variability to increase whitebark pine mortality across our sample areas in the latter 20th century. Thus, we evaluated whether correlations between climatic conditions and growth and defense metrics in the late 20th century would be different for dead whitebark pine compared to live trees. For all climate and time series analyses we established a minimum pair number (5 pairs = 10 trees) to help constrain variability at either end of the time series, where sampling depth was reduced.

Following methods of (Kane and Kolb, 2010) we developed a whitebark pine probability of mortality model using logistic regression. Live and dead whitebark pine were pooled across both sites yielding 144 samples (72 live and 72 dead). Mortality models were evaluated using an information theoretic approach, whereby a variety of candidate models were initially developed from the suite of growth and defense metrics and compared using Akaike's Information Criterion (AIC). We constructed ten models utilizing various combinations of growth and defense metrics following *a priori* assumptions (e.g. that a combination of resin duct size and duct area would collectively influence resin flow and may therefore be important variables influencing survivorship). Model parameters were limited to five variables or less and growth variables for overlapping periods were excluded within any given model to avoid issues of multicollinearity (e.g. 5-year ring area and 10-year ring area). To assess which growth and defense variables were most important in distinguishing between live and dead trees, we also developed conditional density plots using our full dataset.

3. Results

3.1. Growth and defense between live and dead trees

Principle components analysis showed a clear distinction in past growth and defense characteristics between live and dead whitebark pine across all time periods (Figs. 4, S1). Resin duct size, duct area, duct density and relative duct area were the most important variables contributing to the first principle component (PC1), cumulatively describing 45.8% of variability within the data (Fig. 4). Growth (ring

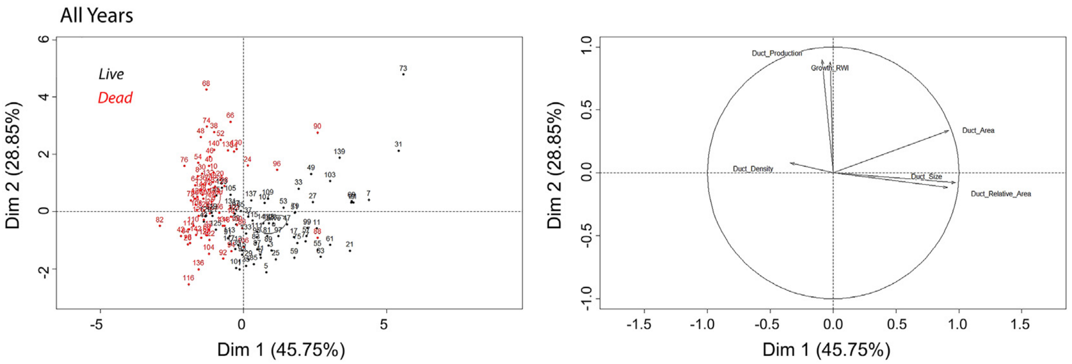

Fig. 4. Principal components analysis comparing growth and resin duct characteristics (production, size, area, density, relative area) for live and dead whitebark pine (144 samples, 72 live, 72 dead). Ellipses are 95th percentile confidence intervals for each grouping (live – black; dead – red). Variables factor map (right panel) illustrates the relative contribution of growth and defense metrics to the ordination. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Age of live and dead whitebark pine at study locations on the Flathead Indian Reservation.

	3LK		BLD	
	Live	Dead	Live	Dead
Age (Range)	72–118	41–100	94–113	44–101
Age (Average)	98 ± 1.9	75 ± 3	105 ± 0.9	77 ± 1.9

Note: Majority of trees died during late 1960s–1990s and exhibited signs of beetle activity (J-shaped galleries on tree bole and blue-staining in increment cores). Overall trends in growth and defense metrics were similar at each site, so the full suite of data was merged for analysis ($n = 144$ trees).

area) and resin duct production had the greatest contribution to PC2, cumulatively describing an additional 28.9% of variability within the data (74.7% total variability; Fig. 4) (Table 1).

Whitebark pine that had died had grown 22% faster (p-value < 0.0001) than living trees during the full record, although this pattern was driven by earlier years (1911–1975; Figs. 5a, 6a). In the 20-years preceding mortality, growth in whitebark that died declined by 26% relative to live trees, especially post-1975 (Fig. 5a). Dead whitebark pine also produced more resin ducts compared to live trees over the full record (20% greater production; p-value < 0.0001; Figs. 5b, 6b). This relationship declined (by 10%) in the 20-years preceding mortality, with the greatest difference occurring during a small interval from around 1990-2000 (Fig. 5b). However, despite producing more resin duct structures on average, the resin ducts were smaller for dead whitebark pine (56% smaller on average) compared to live trees (p-value < 0.0001; Figs. 5c, 6c). Similar to growth, duct size showed an increasing trend post-1975, where duct size in live trees continued to increase relative to dead trees (Fig. 5c).

Resin duct area was also greater in live trees across the full record (48% increase; p-value < 0.0001; Figs. 5d, 6d) and duct area showed a similar post-1975 trend, with increasing area in live whitebark pines relative to dead trees (Fig. 5d). In contrast, resin duct density was greater in dead trees (18% greater; p-value = 0.0149; Figs. 5e, 6e) and post-1975, duct density continued to increase in dead whitebark pine throughout the remainder of the record (Fig. 5e). Relative duct area (% of annual ring occupied by resin ducts) was significantly greater in live whitebark pines (57% increase; p-value < 0.0001; Figs. 5f, 6f, 7). Unlike the other growth and defense metrics, there was no clear temporal trend evident for relative duct area (Fig. 5f).

The two most significant metrics influencing tree survivorship were resin duct size (mm^2), and relative duct area (% of annual ring). Whitebark pine trees that are able to produce larger resin ducts (> 0.001 mm^2) with greater overall duct area ($>$ 10% annual ring) had a significantly greater chance of survival (~80%; Fig. 8).

The best mortality model included resin duct size within the 5-years prior to mortality and relative resin duct area across the full record (all overlapping years of live/dead trees; Table S1). The top five best performing mortality models all included relative duct area (for the full record), highlighting the importance of this metric in differentiating live and dead trees (Figs. 7, 8). The top performing models also included a combination of resin duct size and duct area across the 5-year and 10-year windows (Table S1). The only growth variable significant in the top five models was growth in the 5-year window (RWI; Table S1).

Resin duct production was positively correlated with radial growth for both live and dead trees, indicating that increased growth corresponds with increased resin duct production ($R^2 = 0.36$; p-value < 0.0001; Fig. S2). Duct area was also positively related to radial growth, although this relationship was stronger for dead trees (live: $R^2 = 0.16$; p-value = 0.0003/dead: $R^2 = 0.43$; p-value < 0.0001). Duct size was also positively related to growth in dead trees, though more weakly ($R^2 = 0.1$; p-value = 0.0038) with no real relationship for live trees ($R^2 = 0.02$; p-value = 0.1371; Fig. S2). For duct density, we found a negative relationship with growth for both live ($R^2 = 0.21$; p-value < 0.0001) and dead ($R^2 = 0.05$; p-value = 0.0351) trees (Fig. S2).

3.2. *Influence of climate on growth and defense*

We found differences in the response of live and dead whitebark pine trees to climate across our study sites, particularly in the latter 20th century (Fig. 9, Table S2). Both live and dead trees responded notably to the winter season (in particular winter precipitation and z-PDSI). For instance, growth of live trees was negatively correlated with winter precipitation (-0.41; p-value < 0.0001) and winter z-PDSI (-0.38; p-value = 0.0002), with the strength of this relationship increasing in the latter 20th century (Table S2; Figs. 9, S3). The negative correlation of growth with positive values of z-PDSI indicates reduced growth during wetter (non-drought) years. This response was much greater in live trees, driven in part by a strengthening of these relationships post-1960 for live trees and a simultaneous weakening of these relationships for dead trees during the same time period (Table S2; Figs. 9, S3). Similarly, duct production, duct size, and duct area were negatively correlated with winter precipitation and z-PDSI for live and dead trees, suggesting that during wetter winters whitebark pine trees produced fewer and smaller resin ducts, with a reduction in total resin duct area, although the overall strength of these correlations were modest (Table S2; Figs. 9, S3). These relationships were also much stronger for live trees, with a strengthening of these trends post-1960 and a simultaneous weakening of these relationships for dead trees in the latter 20th century (Table S2; Figs. 9, S3).

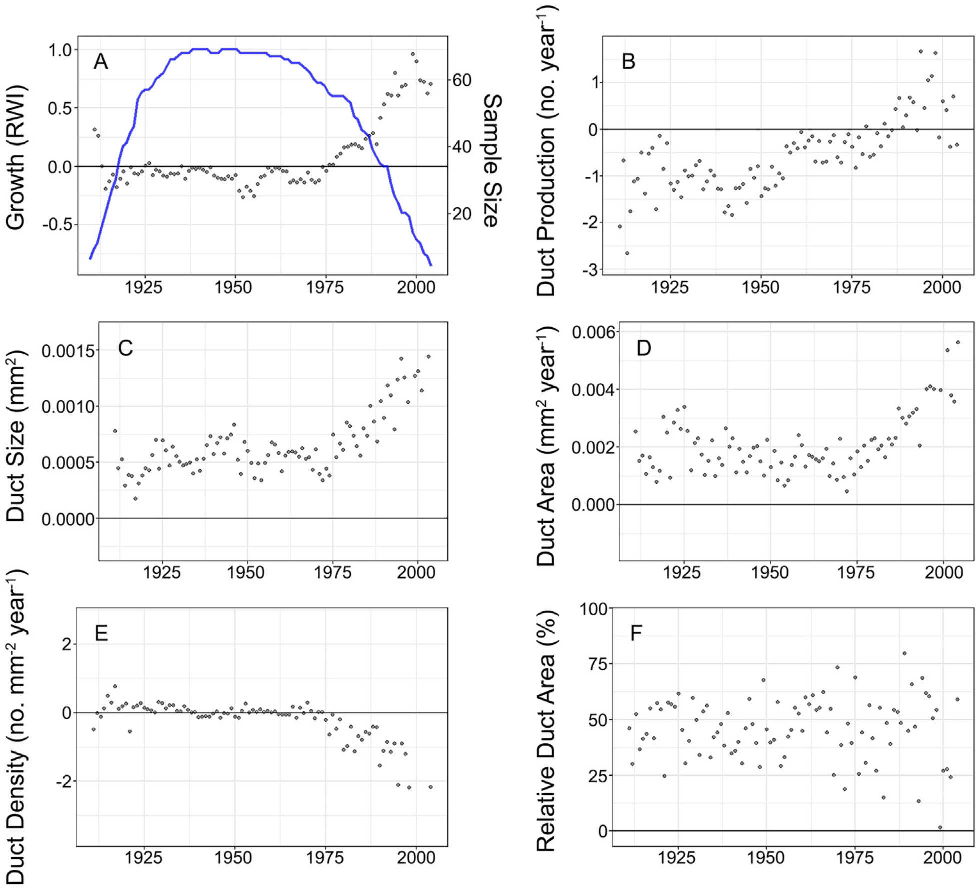

Fig. 5. Time series plots showing the difference in growth and defense metrics between live and dead whitebark pine (144 samples, 72 live, 72 dead). Each point represents the difference in growth/defense metrics for a pair of trees (1 live/1 dead). Points with positive values reflect a greater response for live trees while points with negative values reflect a greater response for trees that ultimately died (formula = [live tree metric] – [dead tree metric]). Blue line in upper-left plot illustrates sample depth across the time series. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

During the spring season, temperatures were positively correlated with growth across both live (0.36; *p*-value = 0.0003) and dead (0.19; *p*-value = 0.05) trees although this relationship was weak post-1960 for dead trees (Table S2; Figs. 9, S4). Growth was negatively correlated with spring z-PDSI for both live (−0.11; *p*-value = 0.312) and dead (−0.26, *p*-value = 0.013) trees (such that wetter years were associated with reduced growth), with the strength of this relationship declining in the latter 20th century, particularly for live trees (Table S2; Figs. 9, S4). Duct production, size, and area were also negatively correlated with spring precipitation and z-PDSI for both live and dead trees, however, this shifted to positive correlations for duct size/area in live whitebark pine in the latter 20th century (Table S2, Figs. 9, S4). Duct area positively correlated with spring temperatures for live (0.24; p-value = 0.019) and dead (0.14; p-value = 0.175) trees, although this relationship faded for dead trees in the latter 20th century (Table S2; Figs. 9, S4). This indicates that whitebark pine trees produced fewer and smaller resin ducts, with a reduction in total duct area during wetter spring seasons; however, these trends have weakened substantially post-1960, possibly due to an earlier onset of spring and changing seasonality in the Northern Rocky Mountains over the past several decades (Pederson et al., 2009, Pederson et al., 2011a, Pederson et al., 2013).

We did not find any significant correlations for growth and summer precipitation or summer z-PDSI in either our live or dead trees, although there was a generally stronger relationship (increased growth with increased moisture) in the early 20th century. Resin duct production in live whitebark pine trees was negatively correlated with summer precipitation (−0.26; p-value = 0.012) and summer z-PDSI (−0.28; p-value = 0.006), such that wetter summers translated to reduced duct production. For dead trees, duct size and duct area correlated negatively with summer precipitation and z-PDSI, whereby wetter summers were associated with decreased duct size/area, although these relationships were strongest in the early 20th century (Table S2, Fig. 9).

4. Discussion

Consistent with previous research (Kane and Kolb, 2010, Ferrenberg et al., 2014, Hood et al., 2015), we found that live and dead trees exhibited notably different growth and defense characteristics. In support of our hypothesis (H2), live whitebark pine produced larger resin ducts with a greater annual investment in resin-based defenses than the whitebark pine that died. Over the entire time series, resin duct size, duct area, and relative duct area were greater in live whitebark pine. In contrast, and counter to our hypothesis (H1), whitebark pine that died exhibited greater growth over the full time series than their live counterparts and also produced more resin duct structures on average. The increased growth was pronounced early in the record (~1919–1975) and shifted notably after 1975, whereby growth declined sharply. While those trees that died produced a greater number of resin ducts on average and consistently had a higher density of resin ducts across all time periods, the relative area of resin ducts was lower than live trees at both sites (Figs. 5–7).

Resin duct size, duct area, and relative duct area were the most important variables influencing whitebark pine survivorship (Fig. 8). Trees producing larger ducts with a greater overall percentage of annual carbon investment were far more likely to survive disturbance events at each of the study sites (Figs. 7, 8). The presence of larger resin ducts and greater overall resin duct area in live trees could be associated with an increased capacity to mobilize oleoresin in response to attack or infection and may be a factor in the ability of live trees to endure numerous disturbance events over time. Although dead trees produced more resin duct structures the ducts were smaller with less overall area, which might have been insufficient to produce, store, and mobilize adequate amounts of oleoresin in response to wounding by

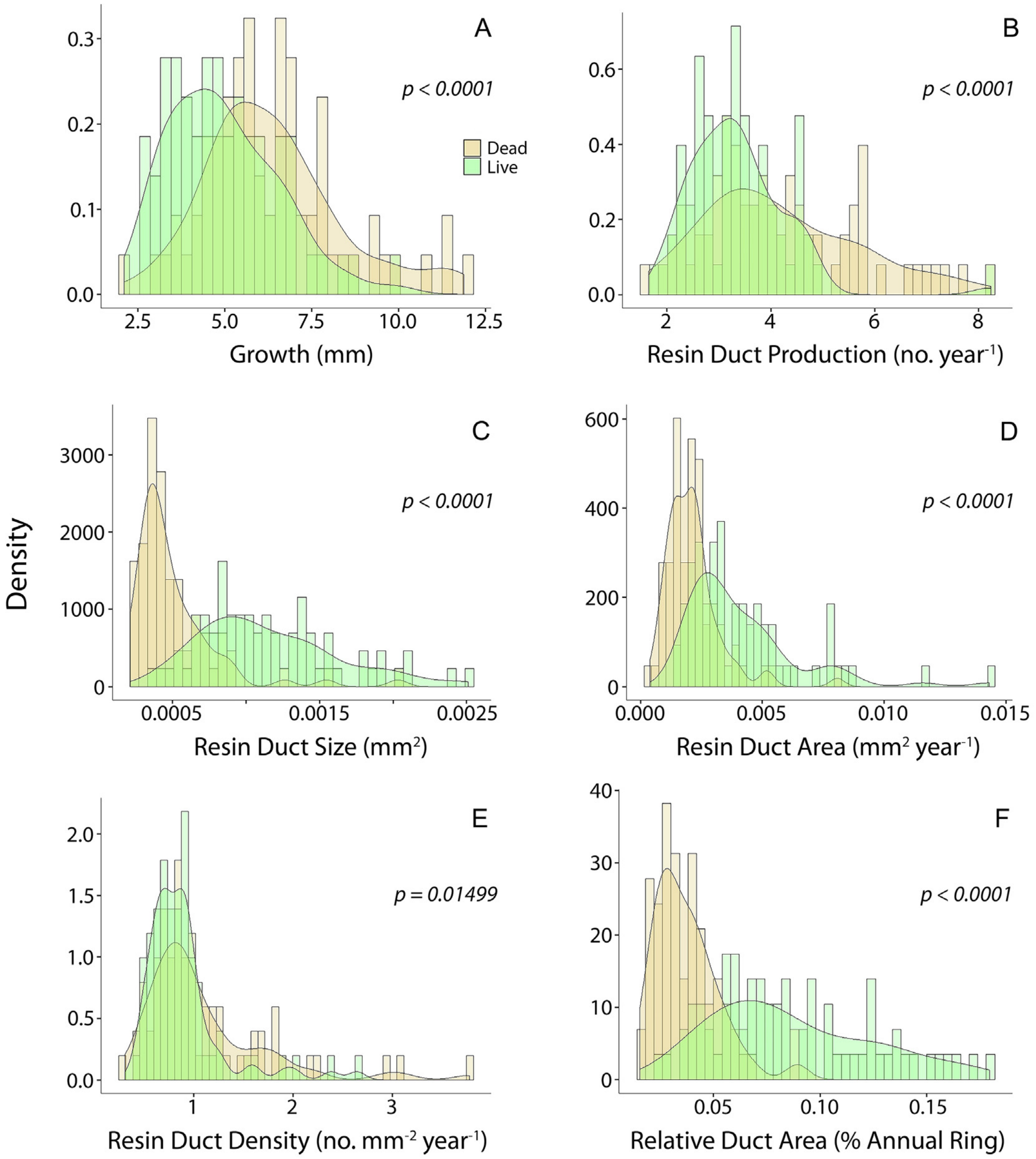

Fig. 6. Kernel density plots for growth and defense metrics across pairs of live and dead whitebark pine. These plots visualize the distribution of samples (depicted as vertical bars) over each continuous variable with a smoothing kernel (smooth lines with shading) applied to assist in visualization of the distributions. Reported *p*-values are from Wilcoxon's paired t-test comparing each metric across live and dead whitebark pine trees.

bark beetles and blister rust infection (Hood and Sala, 2015). This reduced resin flow in dead trees could be linked to lowered defense and higher mortality despite increased density of ducts, particularly in the years leading up to death (Fig. 8).

Importantly, our results suggest that whitebark pine trees that invest a relatively greater amount of resources into the production of constitutive resin-based defenses have a higher probability of surviving disturbance events. This parallels previous research on other conifers (Kane and Kolb, 2010, Ferrenberg et al., 2014, Hood et al., 2015, Hood et al., 2016). Hood and Sala (2015) found that faster growing ponderosa pine produced fewer but larger resin ducts. Similarly, Hood et al. (2015) showed that ponderosa pine that survived bark beetle attack produced larger resin ducts with greater duct area and relative duct area compared to trees that were killed, while Kane and Kolb (2010) reported that ponderosa pine that survived drought and escaped bark beetle activity produced larger resin ducts with a greater relative duct area than trees that died. Gaylord et al. (2015) found that surviving piñon pine produced fewer annual resin ducts than trees that died but these ducts were also larger with a greater relative duct area, similar to our findings. Kläy (2011) also found surviving piñon pines to have larger resin ducts with greater relative area.

In contrast to our results, Kane and Kolb (2010) found that ponderosa pine that persisted through stand-level bark beetle activity produced more resin ducts and had a greater density of resin ducts than dead trees with no detectable difference in growth between live and dead pairs. Similarly, Ferrenberg et al. (2014) found that surviving lodgepole and limber pine both produced more resin ducts and had a greater density of resin ducts than dead trees while surviving limber pine also produced smaller resin ducts than their dead counterparts. Additionally, while slower growth appeared to confer defense benefits in our study, Gaylord et al. (2015) found that live trees exhibited faster growth rates than dead trees. Kläy (2011) found that surviving piñon pine produced more resin ducts with no detectable difference in duct density between live and dead trees, whereas we found resin duct density and numbers where comparable for live and dead whitebark pine. However, it is important to note that our live whitebark pine trees

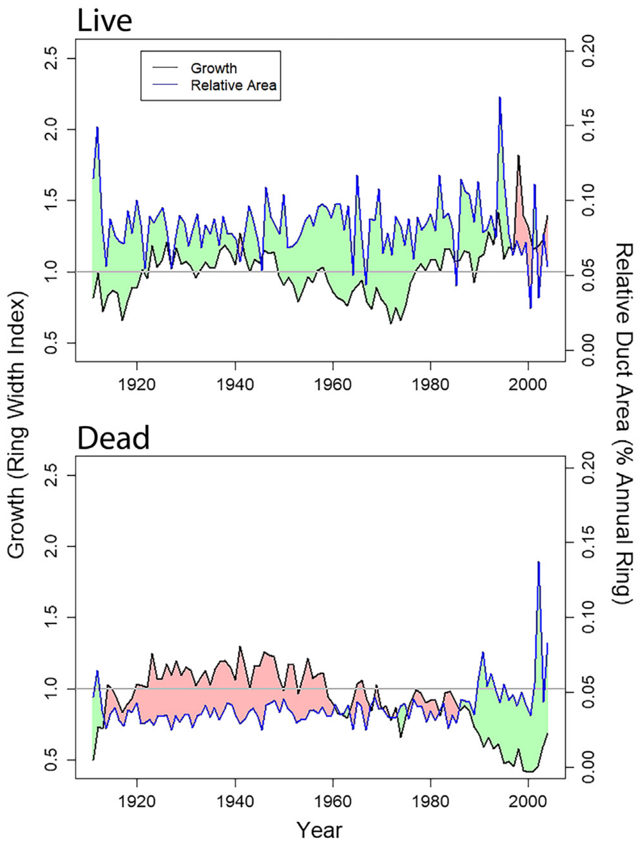

Fig. 7. Time series plots of growth (ring width index) and relative resin duct area (% annual ring) for live (top) and dead (bottom) whitebark pine. The blue line corresponds to relative duct area while the black line corresponds to growth (values above 1 indicate above average growth and values below 1 indicate below average growth). Green shading suggests a greater investment in resin duct defenses relative to growth (higher % of annual ring dedicated to resin duct structures) while red shading suggests a lower relative investment to growth (lower duct area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

did not show any direct evidence of active bark beetle attack and thus, our observations do not reflect a change in growth and defense relationships post-selection. Rather, our results suggest a potential role of growth and defense anatomy in relation to host-identification and host-selection, whereby trees that produced larger resin ducts with a greater annual investment in resin duct features (relative to growth) persisted through stand-level bark beetle activity that resulted in high levels of mortality across our study sites.

The positive relationship we found between radial growth and resin duct production (number of ducts and size of ducts) is consistent with the idea that growth is positively related to duct number (Rigling et al., 2003, Kane and Kolb, 2010, Ferrenberg et al., 2014, Hood and Sala, 2015, Westbrook et al., 2015) and size of resin ducts produced (Ferrenberg et al., 2014, Hood and Sala, 2015). The positive correlation of these defense metrics with increased radial growth suggests factors (e.g. resource availability and climate) that control growth also modulate resin duct structures for both live and dead trees (Fig. S2) (Hood and Sala, 2015, Huang et al., 2019, Mason et al., 2019). The higher relative investment in defense we observed in live trees (increased duct production, size, and area) could reflect a marginal tradeoff with growth as a function of the nutrient-limited, high-elevation environments characteristic to whitebark pine. For instance, when growth is constrained (by resource limitation) photosynthesis continues to produce carbon compounds and this ‘carbon surplus’ may then be allocated toward resin-based defenses, as suggested by the growth-differentiation balance hypothesis (Stamp, 2003). Alternatively, the live trees may have survived due to more beneficial microsites and/or underlying genetic differences that favor greater investment in resin-based defenses relative to growth, even under resource limitation.

The negative relationship between resin duct density and radial growth suggests that faster growing trees exhibit a lower overall investment of annual carbon into resin duct structures relative to xylem (decreased duct density), despite producing larger resin ducts (Fig. S2) (Kane and Kolb, 2010, Hood and Sala, 2015, Moreira et al., 2015). Our results weakly suggest that slower growing trees invest a proportionally greater amount of annual carbon into resin duct structures than structural carbon, highlighting possible increased value of defending critical tissues in the resource-limited settings typical of whitebark pine forests, as suggested by the resource allocation hypothesis (Endara and Coley, 2011) (Fig. S2). While our study was not designed to explicitly test either the growth-differentiation balance or resource allocation hypotheses directly (Hahn and Maron, 2016), they do provide a valuable framework within which we can evaluate growth and defense tradeoffs. The positive relationship between growth and resin duct production, yet negative relationship between growth and relative duct area, highlight the need to utilize both standardized and non-standardized resin duct metrics proposed by Hood and Sala (2015) to understand how physiological tradeoffs influence survivorship under different selective pressures.

4.1. Influence of climate on growth and defense

A negative relationship was found between winter precipitation and drought conditions (winter z-PDSI) and tree growth and all resin duct characteristics (Fig. 9). This was particularly true for live whitebark pine trees. The strength of these correlations increased post-1960. While the overall correlations are modest, they suggest that years with abundant winter precipitation, and winter seasons preceded by short-

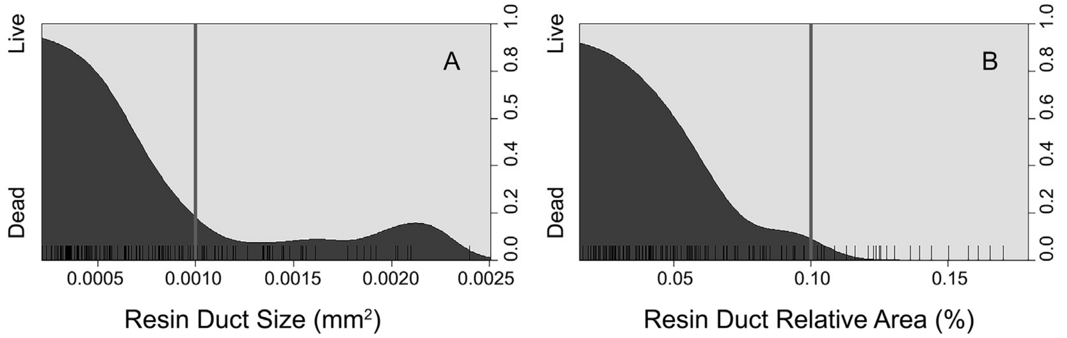

Fig. 8. Conditional density plots describing the probability of mortality in relation to principle resin duct metrics (A) resin duct size; mm^2 and (B) relative resin duct area; % annual ring for 144 whitebark pines (72 live and 72 dead). Light shading reflects live trees while dark shading reflects dead trees. Vertical black bars along the x-axis represents the distribution of samples. See supplementary info for model selection.

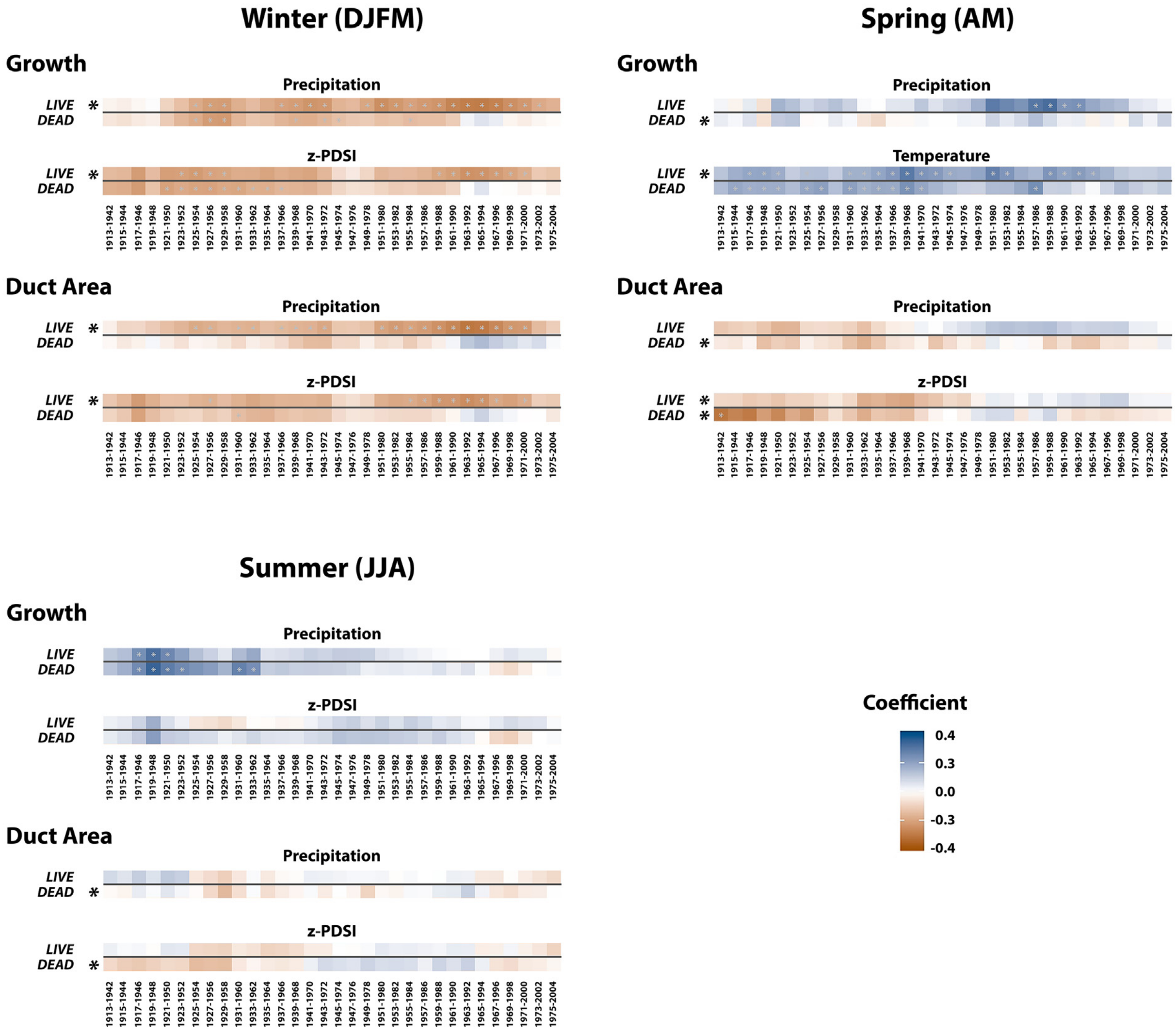

Fig. 9. 30-year moving correlation windows for seasonal climate data (winter/spring/summer). Top panel for each seasonal window: correlations of growth and climate (precipitation/z-PDSI/temperature) for live and dead trees. Bottom panel for each seasonal window: correlations of duct area and climate for live and dead trees. Statistical significance for the full time series (1911–2004) is represented by a '*'.

term drought, could predispose whitebark pine to future mortality by reducing their capacity to fix carbon, limiting subsequent investments in both growth and defense. The modest, negative correlations between reduced growth, defense, and winter precipitation could be a result of increased snowpack, which would reduce photosynthetic activity into the growing season, until the snowpack has ablated and temperatures have increased sufficiently for photosynthesis (Wilson, 1964, Neuner et al., 1999, Vaganov et al., 1999). When temperatures are low and the soil is frozen, which is more likely at higher elevations, photosynthesis is reduced and trees are at an increased risk of xylem cavitation (Sperry and Robson, 2001, Sparks and Black, 2018). This could limit assimilation by reducing water uptake and nutrient transport, delaying annual growth and production of chemical defenses. These results highlight the need to investigate how snowpack, temperature, and precipitation might influence high-elevation conifers differently than low and mid elevation conifers.

Seasonal changes in precipitation, temperature and short-term drought during the spring and summer months was also weakly correlated with growth and defense metrics for both live and dead whitebark pine, however, these results were more nuanced (Fig. 9; Table S2). The strongest relationship was between spring temperatures and growth (positive correlation) and was most pronounced for live trees. In contrast, spring precipitation and z-PDSI (drought) showed a weak negative correlation with growth, resin duct production, duct size, and duct area. The strength of these relationships declined post-1960 and even switched to positive, albeit not statistically significant, correlations in live trees in the latter 20th century. Summer precipitation weakly correlated with increased growth in live and dead trees in the early 20th century, however, this relationship further declined in the latter part of the record. These data weakly suggest a transition from positively correlated growth in summer during the early 20th century to positively correlated growth in spring in the latter part of the record – a trend that may be related to shifts in late 20th century climatic conditions. For instance, earlier snowpack melt and decreased snowpack levels observed in the Northern Rocky Mountains over the past century (Pederson et al., 2009, Pederson et al., 2011b, Pederson et al., 2013) could facilitate earlier photosynthesis and carbon acquisition in late winter/early spring.

The decoupling of climate relationships between live and dead trees in the latter 20th century may also result from increasing stress from cumulative impacts of mountain pine beetle and white pine blister rust, whereby infected trees and trees targeted by beetles allocate as many resources as possible to defense (evidenced by increased duct density) despite the potential need to allocate resources to survive droughts and fire (Table S2; Figs. S3, S4). It is likely that a combination of blister rust (introduced to the Flathead region circa 1950) and/or endemic bark beetle activity (particularly pronounced from the 1960s to 1990s) impacted dead trees. These stressors would have reduced their capacity to fix carbon via photosynthesis due to crown reduction (in the case of blister rust infection) and depleted carbon reserves in the formation of defensive compounds during times of increased beetle pressure. High incidence of blister rust on individuals found in this study indicate white pine blister rust was a significant mortality agent at these sites. These same events could have created favorable growing conditions for the live trees (reduced competition and increased available sunlight) facilitating increased growth and greater allocation of carbon to resin defenses. This is supported by the observed temporal trends in growth and defense metrics (Fig. 5) whereby growth, duct production, duct size and duct area all decreased in dead trees in the latter 20th century while duct density increased. Changes in the relationship between growth and defense and climatic conditions over time also support the idea that multiple disturbances combined to impact whitebark pine individuals at our sites in the late 20th century as we detected a decoupling of growth and defense relationships with climate variables for live and dead trees post-1960 (Figs. S3, S4). The potential shift in response of tree growth and defense in the late 20th century highlights the need for a more thorough investigation of potential physiological responses of plants to dynamic disturbance/climate interactions that have occurred over the past four to five decades.

5. Conclusions

The differences in growth and defense characteristics that we observed between live and dead trees suggests that individuals within whitebark pine stands exhibit genetic variability associated with a range of physiological strategies. In the absence of disturbance, individuals that invest a greater amount of resources towards growth relative to defense experience a fitness benefit allowing individuals to more readily outcompete neighboring vegetation (Herms and Mattson, 1992, Stamp, 2003, Moreira et al., 2014, Moreira et al., 2015, Moreira et al., 2016). Conversely, during periods of heightened insect activity a greater investment in defensive features can increase the probability of survival (Kane and Kolb, 2010, Ferrenberg et al., 2014, Hood and Sala, 2015, Hood et al., 2015, Hood et al., 2016). Within any given stand of whitebark pine there will be individuals with differing physiological strategies (e.g. those that invest more consistently in growth and those with greater regular investments in defense). It is difficult to state which strategies may yield the greatest benefit at any given time, as the interacting disturbances shaping the evolution of whitebark pine are dynamic in both space and time. This supports the well-established premise that maintaining genetic variability in populations is essential for species to persist through varying conditions, especially a species in harsh, highly variable, and disturbance prone alpine environments (Six et al., 2018).

Whitebark pine individuals within both of our sites appear to exhibit differing strategies in the allocation of resources toward growth and defense. Live trees that persisted through 20th century disturbance events produced larger resin ducts with a greater overall annual duct area relative to growth. In contrast, those trees that died invested more into growth, at the expense of defense. Both strategies involve tradeoffs that can confer fitness benefits under different circumstances. As defensive features are energetically expensive to produce and maintain it is difficult to generalize what strategies may be most appropriate under what circumstances. This is an important point when considering contemporary breeding and planting programs, which have been identified as major restoration initiatives in many jurisdictions (Sniezko, 2006, Keane et al., 2012). Within these programs seedlings are traditionally selected for based on growth-related characteristics with little consideration for defensive physiology (White et al., 2007). Our results lend insight into resin duct characteristics that may be beneficial to increasing survivorship and promoting whitebark pine retention, which is particularly important given the sensitivity of whitebark pine to unforeseeable changes in disturbance regimes.

It is becoming increasingly clear that genetic variability and specific traits that are associated with this variability is often an emergent property of the population of trees within a forest stand or landscape yet the full implications for maintaining this variability under rapidly changing biophysical conditions are perhaps not fully appreciated. This is especially true for long-lived sessile species, which face numerous selective pressures of varying frequency and intensity over their lifetime (de la Mata et al., 2017). The specific suite of interacting factors influencing individuals are unique in space and time and work in concert to increase genetic variability within and across populations (Six et al., 2018). Whitebark pine forests have persisted for thousands of years through dramatic changes to climate. The cumulative selective forces acting upon them, such as insects, pathogens, and abiotic disturbances, have likely resulted in the persistence of a broad suite of physiological strategies with benefits under different conditions (Dmitriew, 2011, Monro and Marshall, 2014, Six et al., 2018). Our results further support the idea that maintaining genetic variability and the traits associated with this variability may be critical for species that experience a complex array of biophysical and biological stressors across space and time. Thus, management prescriptions that focus on favoring genotypes that may be the most fit under one set of conditions may lead to heightened vulnerability under complex and difficult to predict climate-disturbance feedbacks and interactions that forests will experience into the future (de la Mata et al., 2017). This may be especially true for forests in harsh, high-elevation settings. Hence, exhibiting one strategy (growth or defense) for surviving an array of stressors (fire, drought, disease) may undermine the capacity for adaptive response to an uncertain future (Dmitriew, 2011, Monro and Marshall, 2014). This observation highlights the need for forest resource managers to better understand how actions might support or undermine genetic variability in forest systems. Specifically, managers might support efforts that maintain genetic variability by: 1) allowing for natural whitebark regeneration following disturbance, 2) limiting post-disturbance impacts (e.g. salvage logging and/or post-fire treatments that undermine natural regeneration, and 3) avoiding blanket prescriptions that preselect for specific traits that may be advantageous under certain conditions yet detrimental under (often unforeseen) future conditions. For instance, while breeding for whitepine blister rust resistant whitebark pine trees has been recognized as one of the primary objectives for expanding rust-resistant strains across management areas, the focus on this one aspect of whitebark physiology may undermine adaptability to other future stressors. For example, rust-resistance may come at the expense of adequate resin duct defenses or reduced growth, which could predispose future whitebark pine populations to unforeseeable shifts in disturbance dynamics. Ultimately, natural resource managers should be cognizant of the capacity (often not well understood) for the genetic variability in whitebark pine forests to provide adaptive responses to complex disturbance, biophysical and biological interactions, now and into the future.

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 data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117736.

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