

ARTICLE

Divergent growth-differentiation balance strategies and resource competition shape mortality patterns in ponderosa pine

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Abstract

Dynamic resource availability leads to trade-offs among functions in plants. The growth-differentiation balance hypothesis (GDBH) predicts greater allocation of carbon to defense than growth when resources are scarce, with optimum defense production occurring at a point between the minimum and maximum growth rates. While the GDBH has been widely tested, consideration of phenotypic variation in rates for which defense is traded for growth and what this variation means for plant resistance remains rare. For defense, pines produce and store oleoresin in “resin ducts.” Retrospective comparisons of resin ducts in pines have revealed that trees with greater numbers, sizes, or areas of xylem resin ducts are more likely to avoid or survive insect attack. We used tree ring chronologies to quantify phenotypic variation in growth and resin duct defenses in pairs of living and bark beetle-killed *Pinus ponderosa* trees in southern New Mexico, USA, and to test the utility of the GDBH for explaining tree mortality. We also assessed the sensitivity of annual growth to climate and competitor density in years preceding mortality in each pair. Survivors had greater growth rates and total cross-sectional areas of resin ducts than trees killed by bark beetles. We did not observe a difference in climate–growth relationships among the groups; however, trees killed by bark beetles suffered negative effects of competition while survivors did not. Growth–defense trade-offs conformed to the GDBH’s prediction of a quadratic relationship; however, the two groups significantly differed in the rate at which defense was traded for increasing levels of annual growth. Our results demonstrate that phenotypic variation in the trade-off between growth and defense could be used to characterize trees that were killed by or survived recent natural enemy epidemics. We hypothesize that the GDBH could be integrated with the characterization of phenotypic variation in growth-differentiation strategies—along with parsing of gene versus

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environment influences on phenotypes—at both local and landscape scales to increase our understanding of patterns of natural enemy impacts in plant populations.

KEYWORDS

climate response, conifer, dendrochronology, plant defense theory, resin ducts, tree mortality

INTRODUCTION

Plant defense theory recognizes that resource pools are often suboptimal and dynamic, leading to variation and trade-offs in plant functions (Stamp, 2003). Simply stated, carbon (C) allocated to one function is not available for others (Rose et al., 2009; Züst & Agrawal, 2017; Züst et al., 2011). The growth-differentiation balance hypothesis (GDBH) is among the more popular frameworks for describing these trade-offs (Herms & Mattson, 1992). The GDBH predicts that resource scarcity limits growth more than photosynthesis, leading to a larger relative allocation of C to secondary metabolism including defense; when resources are plentiful, however, growth outpaces the production of defenses (Figure 1a; Stamp, 2004). Considered in relation to each other, these dynamic rates of growth and defense produce a parabolic curve where defenses reach an optimum midway between the minimum and maximum rate of growth (Figure 1b). The use of the GDBH framework to explain rates of insect attack and mortality in natural settings remains rare yet has the potential to unify theory with observations by considering phenotypic variation in trade-off strategies within and among plant populations (Huang et al., 2020; Lorio, 1986).

Coniferous trees, like other perennial plants, must endure natural enemies to survive and have evolved an array of defenses (Franceschi et al., 2005). Many conifers are attacked by specialized bark beetles (family Curculionidae, subfamily Scolytinae) that live symbiotically with wood-degrading fungi (Raffa et al., 2015). Collectively, beetles and fungi kill all or a portion of their host during the beetles' reproductive cycles and are thought to be a dominant influence on the evolution of conifer defense systems (Raffa et al., 2015). Conifer oleoresin (hereafter “resin”) is a primary defense against natural enemies and can be toxic to or expel attackers (Trapp & Croteau, 2001). Most conifers produce and store resin in specialized “resin ducts,” which, in pines (*Pinus*), occur throughout a tree and exude resin when severed (Franceschi et al., 2005). Retrospective studies of resin duct characteristics in various species have revealed that pine trees killed by bark beetles had smaller or

fewer resin ducts in their xylem relative to survivors (Vázquez-González, Zas, et al., 2020). Despite the protection provided by these defenses, variation in resistance to natural enemies within and among individuals is a ubiquitous feature in pines, as in other plants, and occurs as a result of phenotypic variation and/or in response to environmental and ecological factors such as gradients in resource availability, climate, or competition (Ferrenberg et al., 2017; Hahn & Maron, 2016).

There is broad support for growth-defense trade-offs in plants, including conifers (Huot et al., 2014; Lerdaun et al., 1994; Lorio, 1986; Martinson et al., 2019; Rissanen et al., 2021; Zas et al., 2020). Nevertheless, work in numerous *Pinus* species has revealed a positive relationship among annual growth and resin duct defenses (Vázquez-González, Zas, et al., 2020). Given predicted trade-offs among these functions, some authors use metrics of defense that standardize resin duct measures (e.g., count or cross-sectional areas) by the area of xylem in which they occur to devise a defense: growth ratio (e.g., Hood et al., 2020). This approach typically produces a linear, negative relationship where high rates of growth appear to depress defenses (Hood & Sala, 2015; Vázquez-González, Sampedro, et al., 2020). However, this approach creates two problems for testing predictions of the GDBH. First, it mathematically links the independent and dependent variables under consideration, thereby precluding statistical tests of trade-offs among growth and defense. Second, in forcing a linear relationship, it prevents a test of the parabolic trade-off predicted by the GDBH (Figure 1; Stamp, 2004). If the GDBH is to be tested using tree ring data, an approach that avoids these pitfalls is needed. One possibility, proposed and tested here, is to consider defense production in relation to annual growth rates of individual trees that are relativized to their own lifelong, mean annual growth and then modeling how defenses vary in relation to relative growth rates of each tree. This approach supports tests of the GDBH across individuals with variable attributes (e.g., age, size, or climate sensitivities) or with differing rates of growth linked to variation in resource availability while maintaining independence of the variables in question.

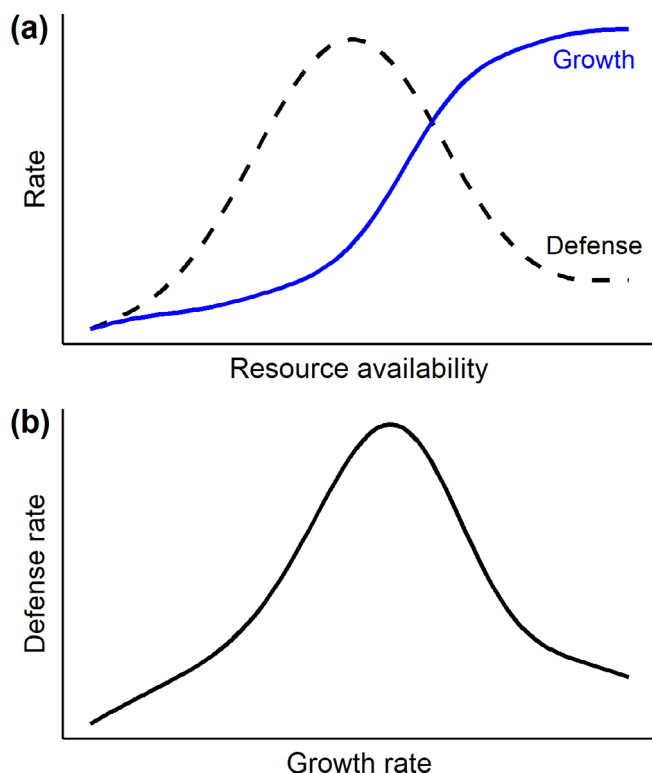


FIGURE 1 Predictions of the growth-differentiation balance hypothesis for (a) rates of plant growth and defense production in relation to resource availability and (b) the relationship among rates of growth and defense. Values used to produce these curves were digitally extracted from Stamp (2004) using WebPlotDigitizer version 4.4 (Rohatgi, 2020).

We examined growth and production of resin duct defenses, along with the sensitivity of growth to climate and local competitor density—both of which can influence resource availability—in pairs of *Pinus ponderosa* (subsp. *brachyptera* Engelm.) trees that had been killed by bark beetles or that survived outbreaks between 1998 and 2008 in southern New Mexico (these groups are referred to at times hereafter as “dead” and “live” trees, respectively, both for simplicity and in reference to their status at the time of sampling). *P. ponderosa* is the most widely distributed species of pine in western North America, ranging from northern Mexico to southwestern Canada, where it strongly shapes the structure and ecology of forests, particularly in semiarid environments characterized by chronic resource limitations (Graham & Jain, 2005). Paired “live” and “dead” trees were matched for similar size and proximity to help in controlling for variation in environment and tree size/age, which can significantly affect resin defense production in pines (Ferrenberg et al., 2017). Using a tree ring chronology, we compared growth and defenses from the same intervals of time in pairs, that is, measures within each pair of trees were for the same calendar years preceding mortality of the “dead”

partner. Our goal was to determine whether trees that survived bark beetle outbreaks exhibited a different growth-differentiation strategy relative to trees killed by bark beetles. In light of widely reported positive relationship among annual growth and resin defenses (Ferrenberg et al., 2017; Vázquez-González, Zas, et al., 2020), and given recent reports of differing drought sensitivity where trees that survived were able to grow more and/or recover more rapidly relative to trees that died in long-term demography studies (Cailleret et al., 2017; DeSoto et al., 2020), growth rate must be considered when quantifying drivers of tree defense and mortality. Thus, we first hypothesized (H_1) that trees killed by beetles and survivors had different sensitivity to interannual climate variation prior to mortality within the pairs. We next hypothesized (H_2) that trees killed by bark beetles produced fewer defenses and had lower growth rates prior to attack compared with trees that survived. Given possible influences of resource competition on growth rates, as part of H_2 , we also quantified the effect of neighborhood density on tree growth rates. Finally, given expected differences among the two groups of trees, we hypothesized (H_3) trade-offs aligned with predictions of the GDBH, where trees that died from beetle attack had lower optima in defense production along a parabolic curve relating resin duct defenses to growth compared with surviving trees, while annual growth rates would have a quadratic relationship with total annual precipitation—a key determinant of resource availability in the semiarid system where our study was performed.

MATERIALS AND METHODS

Site description and sampling

We sampled *P. ponderosa* trees in late summer and autumn of 2018, with some resampled in autumn 2019, near the southeastern boundary of the Gila National Forest, New Mexico, USA. This site was chosen for: (1) its location near the low-elevation edge of *P. ponderosa*'s local range, (2) the occurrence of substantial bark beetle activity between 1998 and 2008, and (3) roads allowing access across private property. This site receives a majority of annual precipitation as a summer monsoon during the warmest period of the year (Appendix S1: Figure S1). Between 1915 and 2008 (the last year of tree rings used in this study) the mean annual precipitation was 468.1 mm, and the mean annual temperature (MAT) was 10.8°C (PRISM Climate Group, 2018). The area was dominated by *P. ponderosa* with *Juniperus deppeana*, *Juniperus monosperma*, *Pinus edulis*, and several species of *Quercus* occurring in low density in the understory. This area was partially harvested in the late 19th century and experienced

a low- to moderate-intensity ground fire prior to the last decade of the 20th century. Canopy trees in the site were primarily recruited in the late 19th or early 20th century.

Samples came from a 550 × 150 m transect, oriented on a northeast–southwest azimuth through a dry arroyo where elevation gently increased from 1982 to 2022 m above sea level, with its center roughly at 32.9607, −108.0455. Sampling location along the transect was determined by the presence of dead trees—all with indications of having been attacked by bark beetles within the past 10 years—which were then paired to the nearest living tree with a diameter at breast height (dbh, ~1.37 m above the ground surface) differing by ≤2 cm; in most cases the paired trees were within 10 m of each other, with the largest separation being approximately 25 m among some pairs. We removed increment cores to the pith at the point where dbh was measured using a 12-mm diameter, two-thread increment borer (Hafslöf, Sweden). We used a laser hypsometer (Nikon, NY, USA) to measure tree height. In cases where the upper portion of a dead tree had fallen to the ground, we located the downed portion, measured the length with a meter tape, and totaled the length and hypsometer values. We collected increment cores from 40 pairs of live and dead trees with all dead trees exhibiting evidence of *Dendroctonus* beetle attack (i.e., pitch tubes on the bark and brood galleries under the bark). In some cases, living trees in pairs had resisted beetles as indicated by the presence of pitch tubes on the bark surface (bark was not removed from live trees). Some dead trees were too decomposed for rings to be identified and one live tree core was damaged during handling, leaving 77 trees (38 complete pairs) with 1 unpaired, live-tree increment core.

We measured competitor density and basal area within a 5-m radius around each tree (a 78.54-m² neighborhood), including all trees ≥1.37 m in height. For trees with multiple stems originating from the ground, we used the cumulative area of all stems at ground level as basal area: an approach applied to *Quercus* and *Juniperus* but not necessary for neighboring *P. ponderosa*. We considered the relationship among the basal area of all competitors and of only *P. ponderosa* and found a significant, positive correlation ($p < 0.05$, $R^2 = 0.88$; Appendix S1: Figure S2). This finding led us to use only the basal area of conspecifics (which were large relative to other species) within neighborhoods during analysis. We chose this approach given the uncertainty over whether small, understory trees had been recruited after mortality of the dead members of tree pairs. We did not collect increment cores from competitors and therefore did not hindcast their basal areas to the time of tree mortality in pairs. However, given the small annual growth rates of trees in our study, the difference between observed and hindcast competitor basal area values is assumed to be minimal.

Dendrochronological and climate data

After collection, we air-dried and mounted increment cores on wooden bases with their vertical orientation maintained and then sanded each into flat cross-sections ending with 500-grit sandpaper. We then scanned all increment cores at 1200 dpi on an Epson V720 flatbed scanner alongside a metric scale and used ImageJ within the FIJI bundle (Schindelin et al., 2012) to measure annual radial growth (in millimeters) of each ring from the pith to 2008 as described in Redmond et al. (2019). We also counted the number of resin ducts in each ring and used ImageJ to measure their cross-sectional areas by placing a freehand polygon around each duct in annual rings from 1980 and ending in the last year of growth in the dead tree of each pair, or in 2008 for the one unpaired live tree. For a small number of dead trees, where degraded wood affected our ability to measure growth and resin ducts, we returned to the study site in autumn of 2019 and collected cross-sectional wedges using a handsaw, prepared each as described above, and placed a 12-mm-wide outline along the longest available axis between the estimated pith location and the bark to mimic the orientation and size of increment cores and then measured each as described above.

We used the NM591 chronology (Black Mountain-PIPO-ITRDB NM591) as a guide for establishing pointer years during visual cross dating and used the “dplR” package (Bunn, 2008) for R to check the accuracy of visual cross dating, build a mean value chronology, and detrend the time series (using a modified negative exponential curve) for the calculation of a ring width index (RWI), which scales annual growth from 0 to 1 within a tree to reduce trends introduced by the change in tree size. We aligned the years of the chronology with climate data for the grid cell of the study site, taking temperature and precipitation data from PRISM (PRISM Climate Group, 2018) and drought severity quantified as the self-correcting Palmer drought severity index (scPDSI) from the National Integrated Drought Information System (NIDIS, downloaded via “drought.gov”). Prior to all analyses, we calculated the age and radius of each tree based on the number and widths of total rings (including those inferred to be missing during cross dating). We back-corrected these measures to reflect values respective to a given year, that is, age and size were corrected across the chronology of a tree by subtracting the values from the subsequent year(s) in the sequence so that age and size were adjusted down, backward through time. Comparisons among “live” and “dead” trees in each pair were performed using only the data from the years aligned among the two prior to mortality of the “dead” tree, that is, no annual rings produced by the “live” tree after mortality in the pair were included in

analyses. The 77 trees we aligned in our chronology had annual growth rings spanning from 1872 to 2008 (the last year in which bark beetle mortality occurred in any of our pairs), with an average series length of 103.8 years (Appendix S1: Figure S3). The chronology included a total of 7991 annual rings with 696 (8.71%) missing rings identified. The mean series intercorrelation was 0.82 for nondetrended and 0.83 for detrended growth values.

As noted above, we paired living and dead (killed by bark beetles) trees for proximity and similar size to control for tree age, environmental, and competition neighborhood conditions. This approach was effective; paired *t* tests revealed no difference in the age ($t = 0.02$, $p = 0.979$), size (measured as dbh; $t = 0.85$, $p = 0.397$), or height ($t = 0.11$, $p = 0.913$) between live and dead trees (Appendix S1: Figure S4). Mean age was 102.4 and 103.1 years in live and dead trees, respectively, while mean dbh was 27.38 and 27.53 cm and mean height was 18.63 and 18.74 m in live and dead trees, respectively. Tree age was significantly, but weakly related to tree size in a permutational linear regression model ($R^2 = 0.21$, $p < 0.0001$; Appendix S1: Figure S5), indicating that detrending procedures predominantly addressed trends in tree growth associated with tree size as opposed to age. There were also no statistical differences in the cumulative basal area ($t = 0.61$, $p = 0.547$; Appendix S1: Figure S4) or individual sizes ($t = 1.67$, $p = 0.102$) of intraspecific competitors in the 5-m-radius neighborhoods around the live and dead trees in each pair.

Data analysis

Analyses were completed in R version 3.6.3. Code for procedures described below is available upon request. To test H_2 , regarding rates of growth and defense production in trees that survived bark beetle outbreaks versus trees killed by bark beetles (also referred to at times as “live” and “dead” trees, respectively, in reference to their status at the time of sampling and for simplicity), we compared radial growth and resin duct count, total resin duct area, and mean resin duct size between live and dead trees using mixed models (i.e., random intercept models). Mixed models were applied to the annual time series data, with paired and nonpaired approaches used to determine if the one unpaired live tree sample influenced results (paired and nonpaired approaches did not yield different outcomes with regard to best-fit models or significance for any test). Paired and nonpaired mixed models were completed with the combination of the “lme4” (Bates et al., 2015) and “lmerTest” (Kuznetsova et al., 2017) packages. Mixed models included “tree_ID” as a random effect to account for the hierarchical structure of repeated

annual measures (i.e., growth rings). Paired models also included “pair_ID” as a random effect to match dead and live members in a pair. Comparisons yielded similar statistical outcomes regardless of the number of years of annual growth considered between 2 and 29 years, with the exception of mean resin duct size, which differed between the groups from 2 to 24 years of growth, but not in retrospective years ≥ 25 . Finally, piecewise structural equation models (SEMs) were created to parse the relative influences of colinear variables—including tree growth, tree age, tree size, and competitor density—on resin duct defenses. SEMs were fit to the live and dead trees groups (i.e., the hypothetical model was fit to live and dead tree data subsets) using the “piecewiseSEM” package (Lefcheck, 2016), which allows for the inclusion of mixed models in the SEM framework, and thus allowing us to deal with the repeated measures data. The conceptual diagrams below indicate the relationships specified in each SEM; model specifications are included as supplemental material (Appendix S1).

To test H_1 , regarding potential differences in climate sensitivity of live and dead trees, we used paired, mixed models as described above for H_2 but with each tree’s RWI series (transformed via square root to improve the data distribution) as the dependent variable and independent variables that included total annual precipitation (TPPT), mean annual drought condition (calculated as the mean annual scPDSI), and MAT; this model was saturated such that interactions (two- and three-way) among climate factors were considered. Using Akaike information criterion (AIC) values, we compared the fit of models with and without “tree_status” (which was also specified as interacting with the climate factors when included in the model) to assess potential interactions among climate drivers and tree mortality/survival groups. We considered three time periods of tree rings using the same model specification: 1915–2008, 1915–1980, and 1980–2008. This split in years was selected because it roughly corresponds to a transition in the Pacific decadal oscillation, which affected annual climate in many regions of western North America.

To test H_3 , we considered the fit of growth and defense data to the predictions of the GDBH using mixed models relating (1) the predicted total area of resin ducts produced to relative annual tree growth with the random effect of “tree_id,” and (2) annual growth rates measured as RWI to total annual precipitation—a correlate of resource availability in this study system—for the same period of time when resin duct measures were quantified (i.e., between 1980 and 2008) with “tree_id” as a random effect. The fit of both sets of models were assessed with and without “tree_status” (i.e., “live/dead” at the time of sampling) to test for difference in phenotype among these

groups. Prior to modeling, relative annual tree growth was calculated by subtracting the population's mean RWI from annual values of RWI for each tree, that is, relative annual growth = $RWI_{\text{annual}} - RWI_{\text{pop_mean}}$. This approach to representing annual growth equates to values <0 indicating periods when a tree was growing less than the long-term mean of the population and values >0 being periods when growth exceeded the mean. Predicted values of total annual resin duct area were computed to reduce issues presented by zero counts in the observed data and were calculated by applying the “predict” function in R to a linear mixed model with observed total annual resin duct area as the dependent variable and with the independent fixed effects of annual resin duct counts, annual radial growth, corrected dbh, corrected age, and the category “tree status.” The model included “tree_id” as a random effect to deal with the repeated measures in the data, while “corrected” values of dbh and age accounted for annual changes by hindcasting these measures based on the observed time series values. Predicted and observed values of total resin duct area were strongly associated ($R^2 = 0.883$, $p < 0.001$; Appendix S1: Figure S6).

To determine whether relationships were best described as linear or quadratic, to test the predictions of the GDBH, models were fit with and without a quadratic term and compared via AIC values using the “performance” package (Lüdtke et al., 2021), which was also used to compute a marginal and conditional Nakagawa's R^2 (Nakagawa & Schielzeth, 2013). For quadratic models to reflect predictions of the GDBH (Figure 1), the relationship between defense and growth was considered as linear versus a second-order polynomial while the relationship of growth to precipitation was considered as linear versus a second- or third-order polynomial. After determining the best-fit candidate model, a “population-level” line of fit was extracted, these data were normalized to range from 0 to 1, and fit to a series of mathematical models using the package “sicegar” (Caglar et al., 2018). This approach determined if the model fits were more accurately described as “sigmoidal,” which would approximate the curve for growth in Figure 1a, or “double-sigmoidal,” which would approximate the parabolic curve in Figure 1b, or alternatively, if the resultant curves approximated neither of these predicted types.

RESULTS

H₁: Climate–growth relationships

Trees that died from bark beetle attack and those that survived outbreaks did not display different growth

sensitivity to annual climate factors including MAT, total annual precipitation (PTT), and drought severity (scPDSI). Best-fit models of tree growth—in this case measured as the relative annual growth rate for each tree—did not retain the “tree status” identifier as a factor (Appendix S1: Table S1); when this factor was included, it did not have a significant influence on tree growth in response to climate for any time period including the time span from 1915 to 2008 (Appendix S1: Figure S7a), years prior to 1980, and years after 1980 (Appendix S1: Figure S7b,c, respectively). Regardless of the years under consideration, the interaction of PTT and MAT, followed by the individual factor of PTT of the year when tree rings were formed, was always the most influential factors on growth, followed by the three-way interaction of PPT, MAT, and scPDSI and the interaction of PPT and scPDSI, which had similar influence in all time periods (Appendix S1: Table S2).

H₂: Growth and defenses among live and dead trees

Trees that survived bark beetle attack had significantly greater rates of growth ($p = 0.0004$; Figure 2a), after accounting for a significant effect of tree size than trees killed by bark beetles. Trees that survived also had larger resin duct sizes ($p = 0.0196$) and greater total area of resin ducts ($p = 0.0351$) than trees that were killed by bark beetles (Figure 2c,d). For comparison, on average, over the 10 years prior to mortality of the dead tree in each pair, trees that survived bark beetles grew at a rate of 1.40 times greater, produced resin ducts that were 1.14 times larger, and produced an area of resin ducts 1.23 times greater than trees killed by bark beetles. The groups did not significantly differ in number of resin ducts produced but surviving trees produced 1.06 times more resin ducts than trees killed by bark beetles over the 10 years prior to mortality within a pair (Figure 2b). The significantly greater total area of resin ducts in trees that survived bark beetle epidemics without a significantly greater number of resin ducts underscores the investment in larger versus more resin ducts as a general trend in survivors relative to trees killed by bark beetles.

We used piecewise SEMs to quantify and parse the influences of tree growth, age, size, and intraspecific competition on resin duct defenses. SEMs for trees that survived the bark beetle outbreak (“live”) and those killed by bark beetles (“dead”) were considered to be reasonably well fit to the data with Fisher's $C = 0.87$ and $p = 0.87$ for the live tree SEM, and Fisher's $C = 8.72$ and $p = 0.19$ for the dead tree SEM (p values >0.05 indicate

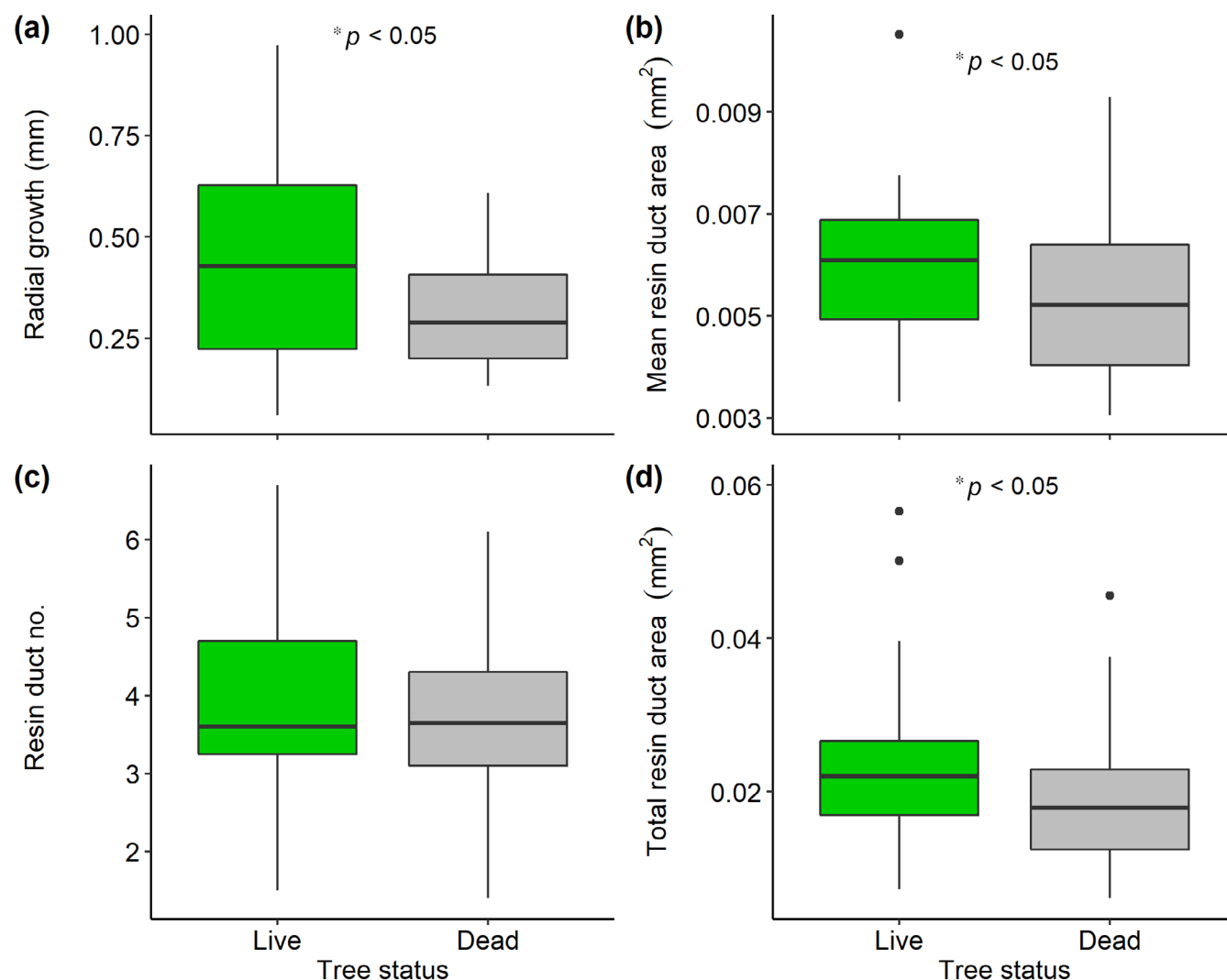


FIGURE 2 Box and whisker plots showing mean values of (a) radial growth, (b) number of resin ducts, (c) mean cross-sectional area of individual resin ducts, and (d) total resin duct cross-sectional area for the last 10 years of annual values in trees that survived bark beetle outbreaks (live) and trees that were killed by bark beetles (dead). The 10-year interval of time was aligned to cover the same calendar years within pairs of live/dead trees, with the last year in each pair's time series being the last, full growth ring in the "dead" member of the pair.

models that are well fit to the data in these tests). The SEMs for both groups of trees revealed significant positive relationships among tree age and size, tree size and annual growth, and annual growth and total area of resin ducts produced each year (Figure 3). Following the paths within the SEMs indicates that as trees age, not only do they increase in size, but they also tend to have greater rates of annual growth relative to younger stages. However, the influence of tree size on annual growth and the influence of tree growth on resin duct defenses were greater in the trees that survived versus those killed by bark beetles (Figure 3). The SEMs also revealed a significant negative effect of competition on annual growth in the trees killed by bark beetles but not in the surviving trees (Figure 3).

H₃: GDBH strategies among live and dead trees

Comparisons of models relating resin duct defenses to relative annual growth indicated that a second-order polynomial that included "tree status" (i.e., live vs. dead) was a better fit to the data relative to alternative models (Appendix S1: Table S3). The best-fit model showed a significant influence of relative growth rate on total resin duct area produced ($F = 803.6$, $p < 0.0001$) and revealed a significant interaction among tree status and relative annual growth ($F = 3.7$, $p = 0.0238$): an indication of a significant difference in the relationship of growth and resin duct defenses among trees that survived versus trees that were killed by bark beetles. In other

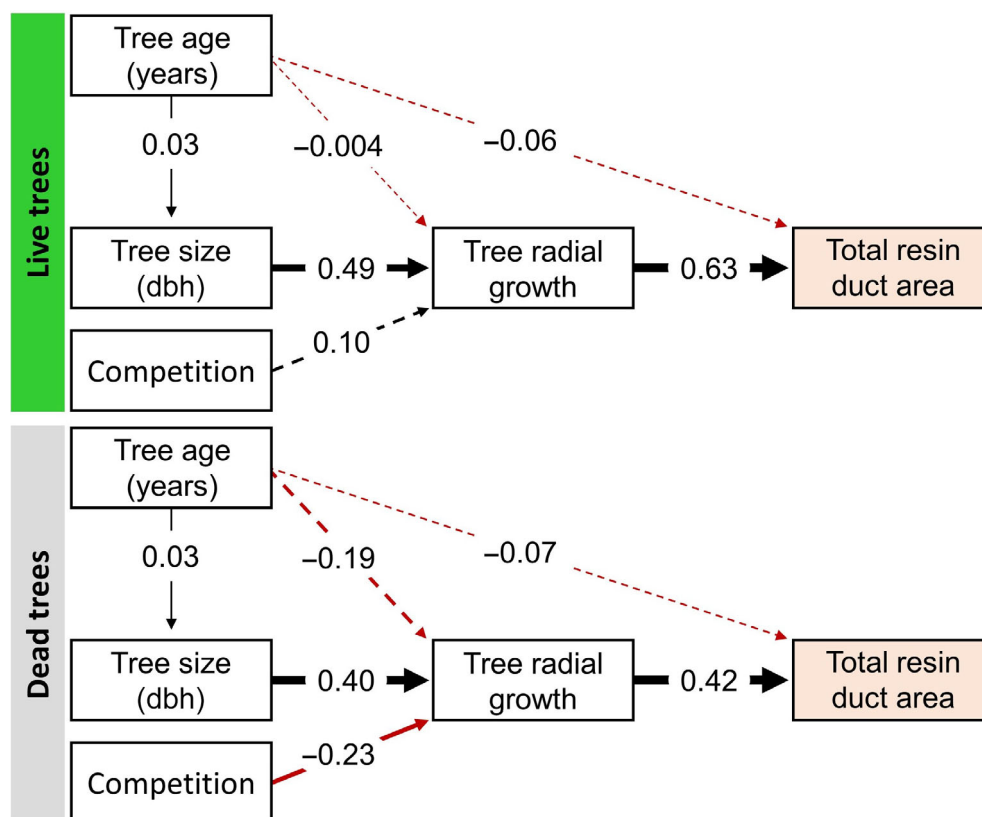


FIGURE 3 Piecewise structural equation models showing the influences (standardized coefficients) of tree age, size (diameter at breast height), radial growth rate, and neighborhood competition (total basal area of conspecifics) for ponderosa pines that survived bark beetle attack (live trees) or were killed by bark beetle attack (dead trees). Black lines show positive effects, red lines indicate negative effects, and solid lines indicate paths considered to be statistically significant ($p < 0.05$); line and arrow widths are scaled to reflect values of the standardized coefficients.

words, the “shape” of the polynomial line of fit differed among the two status groups, signifying different growth-differentiation balance strategies in trees that were killed by bark beetles and those that survived the outbreaks (Figure 4a). Regardless of tree status, the relationship among growth and defense better approximated a second-degree or “double-sigmoid” curve—a downward opening parabola—than a “sigmoid” curve, making it qualitatively similar to predictions of the GDBH (Figures 1b and 4a). For both live and dead trees, the models for a double sigmoid had smaller AIC values of -308.9 and -309.2 , respectively, versus -303.0 and -303.2 for their sigmoid alternatives.

Comparisons of models relating relative growth rates to annual precipitation—considered to be a correlate of resource availability—indicated a third-order polynomial without “tree status” was a better fit to the data than alternative models (Appendix S1: Table S4). The best-fit model illustrated a significant, nonlinear relationship between growth and precipitation ($F = 201.4$, $p < 0.0001$) in the form of a third-degree parabola best described as a “sigmoid” curve (AIC = -159.5) as opposed to a “double

sigmoid” (AIC = -19.5). However, the shape qualitatively differed from sigmoidal relationship predicted by the GDBH (Figures 1a and 4b).

DISCUSSION

Rates of tree mortality have increased worldwide in response to global change (Allen et al., 2015). In western North America, for example, interactions of climate change, land-use history, and landscape features have led to extensive conifer mortality during bark beetle epidemics and droughts (Berner et al., 2017; Ferrenberg, 2016). Efforts to distinguish phenotypic characteristics of trees that survive or succumb to these pressures have received renewed interest in light of global increases in tree mortality (Cailleret et al., 2017; DeSoto et al., 2020). We compared growth and resin duct defense characteristics in pairs of *P. ponderosa* trees that were either killed by bark beetles or survived outbreaks with the aim of quantifying growth-defense allocation strategies among these groups. Despite reported differences in the sensitivity of growth to

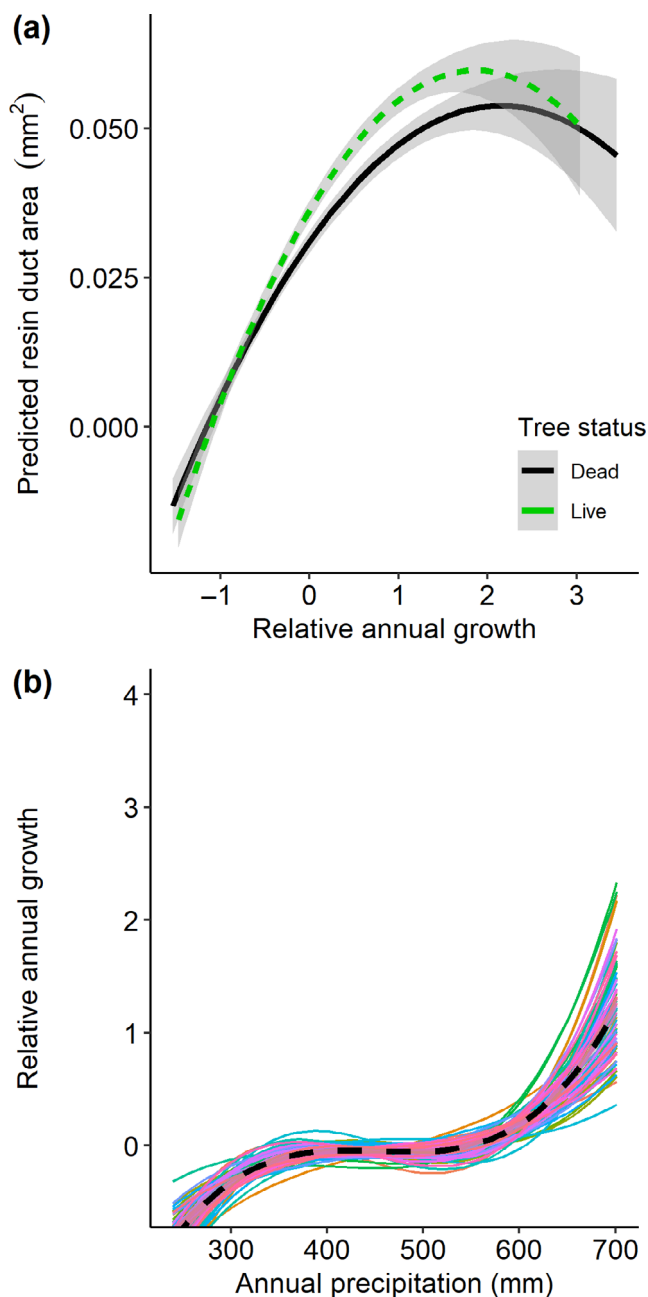


FIGURE 4 (a) Relationships among the predicted total cross-sectional area of resin ducts produced and relative annual growth rate in trees that survived bark beetle outbreaks (live) and those killed by bark beetles (dead); lines illustrate the population response and shading indicates the 95% CI. (b) Relative annual growth rates as a function of total annual precipitation; solid lines with different shades represent individual trees while the dashed black line illustrates the population response.

interannual climate variation among deciduous and coniferous trees that lived or died during recent droughts and natural enemy outbreaks across a wide range of species and climates (Cailleret et al., 2017; DeSoto et al., 2020), we did not find support for our first hypothesis (H_1) of a difference in climate sensitivity among the surviving and

bark beetle-killed trees in our study, leading us to reject a role of climate sensitivity as a primary determinant of the likelihood of survival/mortality of *P. ponderosa* during recent bark beetle outbreaks in our study system. We found support for our second hypothesis (H_2) that *P. ponderosa* trees killed by bark beetles had significantly lower rates of growth and smaller total areas and sizes of resin ducts than trees that survived the epidemic (Figure 2) along with evidence that trees killed by bark beetles suffered negative effects of competition while surviving trees did not (Figure 3). We also found support for our third and primary hypothesis (H_3) that trees killed by bark beetle attack had lower optima in defense production relative to surviving trees (Figure 4a), with the relationship of defense production to annual growth being best described by a quadratic curve in line with the prediction of the GDBH (Figure 1b). Also, in support of H_3 , we found a quadratic relationship of annual growth with total annual precipitation but with a departure in form from the exact prediction of the GDBH (Figures 1a and 4b).

Tree growth and defense relationships

The greater rates of growth and production of resin duct defenses in trees that survived the bark beetle outbreak versus those killed by bark beetles align with the small number of prior retrospective comparisons of growth and resin duct defenses in conifers that survived or were killed by natural enemies (Vázquez-González, Zas, et al., 2020). For the *P. ponderosa* population we examined, differences in growth and total resin duct areas among surviving and bark beetle-killed trees were detectable for any interval of time from 2 to 29 years of annual tree rings and from 2 to 24 years for resin duct size, indicating that these patterns were present for decades prior to the bark beetle epidemics that led to mortality in our pairs of trees. Resin ducts occur in an interconnected network throughout the xylem (Franceschi et al., 2005) and are reported to remain active for up to 20 or more years (Blanche et al., 1992). Thus, the importance of these defenses in shaping susceptibility to natural enemies is best viewed as a multiyear to multidecadal process as ducts produced even decades prior to natural enemy attack could contribute to defense and resistance. Surviving *P. ponderosa* trees in our study system also produced more resin ducts on average than trees killed by beetles, but this difference was not statistically significant. However, the greater total area of resin ducts without a significantly greater number of resin ducts found in surviving trees points to the importance of larger resin ducts for defense against bark beetles and their symbiotic fungi—an outcome now reported for multiple species of pines (Ferrenberg et al., 2014;

Hood et al., 2015; Kane & Kolb, 2010; Slack et al., 2021; Valor et al., 2021; Vázquez-González, Zas, et al., 2020; Zhao & Erbilgin, 2019).

Phenotypic variation in GDBH strategies

As noted above, we found support for our second hypothesis of trade-off among growth and defense reflective of the parabolic curve predicted by the GDBH in both surviving and bark beetle-killed trees, but with different defense maxima among the groups. While this difference among the groups in their maxima of defense relative to annual growth might appear minor, it must be considered in light of the 20-year activity window of individual resin ducts and the network within which they are embedded (Blanche et al., 1992; Franceschi et al., 2005). In other words, by producing more defenses relative to growth in many years—particularly in years when growth is near or above the long-term population mean rate, trees that survived the bark beetle outbreak likely benefited from a multidecadal “defense bank” where small advantages in defense production accumulated over time through the resin duct network and allowed these trees to avoid and/or resist natural enemies during insect epidemics.

Prior work in conifers has provided support for the predictions of the GDBH. For example, drought-stressed *Pinus sylvestris* (var. *sylvestris* L.) trees allocated more C to resin than did irrigated trees (Rissanen et al., 2021), while resin flow and growth were negatively correlated within *Pinus pinaster* (Aiton) (Zas et al., 2020). Further, early studies of resin production in pines across a calendar year produced a parabolic curve that appeared to support predictions of the GDBH, but how production of defenses related to growth during these studies was not reported (Lerdau et al., 1994; Lorio, 1986). Importantly, the interpretation of whether changes in resin defenses measured across time or resource gradients support the GDBH can often remain unclear due to questions of how to quantify defenses, particularly over time in perennial plants (Stamp, 2004). Recent meta-analytical support suggests that resin duct measures—including the metrics of total cross-sectional area, numbers, and sizes that we employed in our study—are accurate measures of defense and resistance against insect natural enemies in conifers (Vázquez-González, Zas, et al., 2020). However, in the absence of measures of rates of other tree functions (e.g., reproduction) or compartments beyond the stem (e.g., needles or roots), it is important to consider potential carbon allocation strategies that might have affected rates of growth or defense and thereby shape apparent trade-offs when comparing growth and resin duct

measures in pine stems. For example, masting events and associated cone/seed production in *P. edulis* have been shown to depress resin duct defenses but not tree growth (Redmond et al., 2019). Studies that simultaneously quantify assimilation rates and/or other vital functions in relation to growth and defense are needed to further elucidate C-allocation strategies in conifers, particularly if we are to quantify the influence of these strategies on tree fitness.

All trees exhibited a quadratic relationship among growth and total annual precipitation—a correlate of resource availability—but the form of this relationship differed from that predicted by the GDBH with no difference among trees that succumb to bark beetles and those that survived. The discrepancy among the prediction of the GDBH and relationship of tree growth and precipitation that we observed is likely driven, in part, by important influences of other abiotic factors that can influence tree growth, such as soil properties, as reported for numerous forest systems (e.g., Soong et al., 2020; Van Sundert et al., 2018). As might be expected, we found that combining the measures of total annual precipitation, MAT, and mean annual drought severity dramatically improved the ability of models to describe tree growth in response to climate (Appendix S1: Tables S2 and S3): an outcome that illustrates the role of climate factors beyond precipitation in dictating annual tree growth. In addition, recent work focused on coniferous tree species' responses to annual precipitation indicates not only different growth responses to precipitation totals and timing within a year across species, but the presence of multiple, potential response types within species that can vary from linear symmetric to curvilinear positive and negative asymmetric in nature (Dannenberg et al., 2019). This presence of alternate climate–growth relationships occurring within and among coniferous species suggests that the GDBH may be too strict in predicting one form of growth-resource strategy and that alternative relationships are likely to be present within and among populations.

Influence of competition on growth and defense

Mortality of conifers at landscape scales has been linked to both density-dependent and density-independent factors, with the age of a forest stand often determining the balance of these factors (Aakala et al., 2007; Acker et al., 2015; Das et al., 2011; He & Duncan, 2000; Larson et al., 2015; Silver et al., 2013). Our study design did not support a characterization of spatial patterns of mortality and was completed in a relatively uniform age class of trees. Nevertheless, we found a negative effect of

conspecific basal area on the growth rate of trees killed by bark beetles and a positive, nonsignificant relationship in surviving trees. Thus, while the groups had qualitatively similar relationships among defense production and tree attributes including age and size, they appear to have differed in their ability to compete for resources in neighborhoods of similar densities. This difference in competitive ability among trees in the surviving and bark beetle-killed groups affected their rates of growth, which, in turn, influenced their production of resin duct defenses and ultimately their rate of trade-off among growth and defenses. While it is unclear what role genes versus environment play in shaping these different trade-off phenotypes, the presence of two subsets of trees with different responses to neighborhood density within a population suggests that frameworks for describing the drivers of tree mortality across the landscape could be advanced through efforts to assess levels and turnover in phenotypic variation. For example, the negative relationship of growth to intraspecific neighborhood density and the subsequent depression of resin duct defenses in trees killed by bark beetles offers a potential approach for quantifying stand-level susceptibility to natural enemies prior to destructive epidemics.

Tree growth and climate sensitivity

As noted above, we did not observe differences in growth sensitivities to interannual climate variation among survivors and trees killed by bark beetles. This result conflicts with reports of different drought sensitivity among trees that died or survived in numerous species of angiosperms and gymnosperms, for example, DeSoto et al. (2020) and Cailleret et al. (2017). However, the effect sizes in these reports are quite small and statistical significance relies on their very large sample sizes, which not only presents a challenge for comparing climate sensitivity among tree groups in studies where sample sizes are less than many hundreds to thousands of trees, but also raises the question of what level of effect size is needed to infer biological relevance from tree ring data. At the same time, studies in congeners of *P. ponderosa* have indicated that both drought-induced and bark beetle-induced mortality can be preceded by a loss of climate sensitivity in annual growth, indicating that some species or population may not exhibit divergent responses to drought or other climate factors (Ogle et al., 2000; Sangüesa-Barreda et al., 2015). Nevertheless, the use of tree ring data may belie or mute differences among resistant and susceptible trees relative to other metrics. For example, comparisons of white spruce (*Picea glauca* [Moench] Voss) trees that survived versus those killed by bark beetles revealed that

growth sensitivity to climate factors was more evident in isotopic measures of water-use efficiency and drought stress than in radial growth (Csank et al., 2016). This approach, however, can still yield conflicting results; comparisons of *P. ponderosa* growth rates and drought tolerances—based on carbon isotopic ratios in annual xylem rings—in trees that either survived or were killed by bark beetles in California, USA, revealed an important influence of annual growth rates but no differences in drought sensitivity among the groups (Keen et al., 2020).

Potential influences of study design and location

In our study, trees categorized as “live” or survivors were similar-sized neighbors to trees killed by bark beetles. In some cases, but not all, survivors had external signs of having been attacked by and resisted bark beetles. Whether surviving trees were attacked by bark beetles or not varies across available retrospective studies. For example, Kane and Kolb (2010) compared *P. ponderosa* trees killed by bark beetles to neighbors that had presumably avoided attack, while in Ferrenberg et al. (2014), surviving trees had been attacked but resisted mortality. While similar approaches, this difference among studies reveals that bark beetles can selectively attack “less-defended” trees yet can err during this selection process and encounter individuals with sufficient defenses to resist beetles and their symbiotic fungi. How these different study designs might affect comparisons of the GDBH among surviving and bark beetle-killed trees, however, remains unclear and worthy of consideration. Understanding the thresholds in defense production that promote bark beetle avoidance versus resistance is important for understanding not only trade-offs among defense and other functions but also how the balance among various functions shapes natural selection and evolution of defense strategies in conifers.

Position on the landscape and ecoclimatic variation are also likely to shape relationships among tree growth and defense as well as responses to climate drivers (Dannenberg et al., 2019). For example, position along an elevational climatic gradient can influence defenses of *P. ponderosa* among other species (Ferrenberg et al., 2017) while interannual climate variation can shape pine reproduction strategies and produce trade-offs among cone production and defenses (Redmond et al., 2019). When considering climate–growth relationships, existing ecological theory predicts that plant growth should be more constrained by resource competition in areas with mild to moderate resource stress (Maestre et al., 2009). Our study was located in a region where *P. ponderosa* genetic

variation is relatively large compared with other portions of the species' range (Potter et al., 2015) and in a system characterized as warm semiarid (e.g., Köppen classifications *Csa* and *Csb*). Common garden experiments with *P. ponderosa* from across this larger region have indicated that individuals from populations from warmer, drier locations tend to perform or survive better under drought conditions than conspecifics with provenance from cooler or wetter climates (Dixit et al., 2021; Kolb et al., 2016). Despite this evidence of local adaptations to climate regimes, to date, studies of conifer growth and defense are more common in forests with relatively "cool" climate classifications (e.g., Köppen classifications *Dfc*, *BSk*, *Dfb*, and *Csb*) than warm semiarid. Understanding how landscape position, particularly in relation to large climatic and resource gradients, interacts with local properties such as neighborhood density to shape growth-defense allocation strategies in light of predictions made by the GDBH requires further study.

CONCLUSIONS

The energetic or carbon "cost" of growth, reproduction, and defense have long been theorized to constrain each other in plants via trade-offs that reflect allocation priorities given limited resources (Züst & Agrawal, 2017). Plant defense theory has sought to explain why allocation to one or more functions is prioritized over another in a given population, species, or community (Stamp, 2003). Phenotypic variation in the forms and rates of trade-offs among important functions in plants is common and when explained by allocation strategies is often assumed to be driven by the combined influences of genetics and ecological factors such as variable resource availability (Endara & Coley, 2011; Glynn et al., 2007; Moreira et al., 2015). Because these causal factors are often viewed as less variable at the local versus landscape scale, the role of phenotypic variation in growth-defense allocation strategies in shaping fine-scale patterns of plant-herbivore interactions have often been downplayed relative to influences of coarse-scale patterns demonstrated across elevational, latitudinal, and continental extents (Carrillo-Gavilán et al., 2015; Ferrenberg et al., 2017; Moreira et al., 2014, 2020; Pearse & Hipp, 2012; Wang et al., 2016). We found that the trade-off among growth and defense in *P. ponderosa* trees of a population inhabiting a shared environment not only conformed to predictions of the GDBH but also that variation in the rate of this trade-off differentiated trees that were killed by bark beetles from those that survived the outbreaks. This variation in allocation strategy among surviving and beetle-killed trees appeared to be caused, at least in part,

by a significant difference in their ability to compete with conspecifics for resources in neighborhoods of equivalent densities. We hypothesize that the GDBH could be applied as a guide for characterizing phenotypic variation in growth-differentiation strategies—along with a parsing of gene versus environmental influences on growth and defense phenotypes—at both local and landscape scales to increase our understanding of patterns of natural enemy impacts within and among tree populations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Ferrenberg et al., 2022) are available from Dryad: <https://doi.org/10.5061/dryad.z612jm6fd>.

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SUPPORTING INFORMATION

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

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