

Tree resistance to drought and bark beetle-associated mortality following thinning and prescribed fire treatments

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ARTICLE INFO

Keywords:

Defense
Forest health
Growth
Resin ducts
Tree vigor
Pinus lambertiana
Abies lowiana

ABSTRACT

Long-term trends show increased tree mortality over the last several decades, coinciding with above-average temperatures, high climatic water deficits, and bark beetle outbreaks. California's recent unprecedented drought (2012–2016) highlights the need to evaluate whether thinning and prescribed fire can improve individual tree drought resistance and reduce bark beetle-associated mortality. Using a thinning and prescribed fire study on the Stanislaus-Tuolumne Experimental Forest in the central Sierra Nevada implemented prior to the drought (2011–2013), we used dendrochronological methods to estimate metrics of tree vigor (i.e., growth and resin ducts) of sugar pine (*Pinus lambertiana* Douglas) and white fir (*Abies lowiana* [Gordon & Glend.] A. Murray bis) among treatments, as well as between trees that died from bark beetle-associated mortality and their paired counterparts that survived. We used tree vigor to estimate drought resistance as the ratio between growth during drought (2012–2016) and pre-drought (2007–2011) for both species. For sugar pine, we also created analogous ratios for multiple resin duct characteristics to evaluate defense during drought. Our findings indicate that lower competition increased growth resistance of white fir, while prescribed fire had negligible impacts on growth. This translated to lower mortality, with live white fir showing higher growth resistance than those that died. While competition did not strongly affect sugar pine growth, greater growth resistance was noted for trees that lived than trees that died. However, reduced competition and prescribed fire increased defense resistance and resin duct density and relative resin duct area were negatively associated with sugar pine mortality. Live sugar pine showed greater defense resistance than dead counterparts particularly under higher levels of competition. These findings suggest thinning can promote or maintain growth during severe drought conditions and prescribed fire can be applied with negligible costs to tree growth while also producing the additional benefit of stimulating defense systems in sugar pine, which may enable them to better survive bark beetle outbreaks. Therefore, susceptibility to bark beetle-associated mortality may be ameliorated through increasing tree vigor with a combination of forest thinning and prescribed fire.

1. Introduction

Although drought is a common occurrence across the world, recent decades of “hotter” droughts have induced rapid, exponential rates of tree mortality in forested ecosystems (Allen et al., 2015). For years, forests in California already exhibited drought vulnerability, with elevated rates of background mortality related to density and climatically-driven tree stress (van Mantgem and Stephenson, 2007; van Mantgem et al., 2009). These signs foreshadowed the massive tree die-off that occurred during an unprecedented drought in California from 2012 to 2016 (Griffin and Anchukaitis, 2014), when an estimated 129

million trees died (USDA Forest Service California Climate Hub, 2017). Regions characterized by high drought stress (i.e. lower elevations, lower latitudes, and areas with greater tree densities) suffered higher mortality (Young et al., 2017; Restaino et al., 2019), with the proximal agent of mortality for most conifers being bark beetles (Fettig et al., 2019).

Although endemic in many forests, bark beetles can become destructive agents of mortality under certain conditions (Raffa et al., 2008). Excessive soil moisture exhaustion may occur during multiple years of drought (Goulden and Bales, 2019), which can inhibit defense mechanisms against bark beetles and predispose trees to bark beetle-

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<https://doi.org/10.1016/j.foreco.2022.120758>

Received 23 August 2022; Received in revised form 17 November 2022; Accepted 22 December 2022

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associated mortality (Gaylord et al., 2013; Kolb et al., 2019). Following a century of fire exclusion, historically frequent fire forests have shifted towards more homogenous structures with higher tree densities (Knapp et al., 2013; Lydersen et al., 2013), increasing the number of potential hosts that are available for bark beetles to colonize and kill (Raffa et al., 2008). Drought intensity is positively linked to bark beetle populations, performance, and attack success (Bentz et al., 2010; Kolb et al., 2016), enabling them to exceed critical thresholds required to kill host trees (Boone et al., 2011). Any combination of these factors can reinforce positive feedback loops, ultimately leading to eruptive beetle outbreaks and contributing to amplified rates of trees mortality.

In the face of density and climatically-driven tree mortality, increasing the resistance to drought stress and beetle outbreaks is a critical management objective. Resistance is defined as the capacity to withstand disturbance by maintaining physiological performance during a disturbance (Lloret et al., 2011). Tree resistance to mortality from drought and bark beetles is often associated with several physiological metrics, including growth and defense. Growth is a commonly used metric for comparing trees that died during drought with trees that survived (Cailleret et al., 2017). Tree mortality is generally preceded by declines in radial growth, with the longevity and strength of those declines varying by species (Kane and Kolb, 2014; Desoto et al., 2020). However, generalizable growth trends related to bark beetle-associated mortality are often obscured by the idiosyncratic nature of host selection (Stephenson et al., 2019; Reed and Hood, 2021), with weak growth signals and abrupt tree death more prevalent during beetle outbreak conditions (Cailleret et al., 2017). Resin ducts are an important constitutive defense system, storing and deploying oleoresins to physically or chemically inhibit insect attack (Franceschi et al., 2005), with resin duct characteristics such as density and area showing a strong relationship to bark beetle resistance (Kane and Kolb, 2010; Hood and Sala, 2015; Slack et al., 2021). The capacity of a tree to resist bark beetle attack increases with greater investment in resin ducts (Kane and Kolb, 2010; Ferrenberg et al., 2014). Lower investment in resin ducts can further pre-dispose trees to mortality during severe drought conditions (Gaylord et al., 2013).

Although thinning and prescribed fire are treatments often designed to meet multiple objectives such as timber extraction and fuel reduction, a beneficial byproduct may include mitigating tree mortality due to drought and bark beetles. Thinning, individually or in combination with prescribed fire, can effectively reduce tree mortality from bark beetles (Fettig et al., 2012; Stark et al., 2013; Hood et al., 2016; Steel et al., 2021) by increasing growth and resin defenses under water stress (Hood et al., 2015, 2016). However, the impacts of prescribed fire alone on tree vigor and mortality have been mixed. In pines (*Pinus* spp.), prescribed fire can stimulate resin flow and resin duct production (Perrakis and Agee, 2006; Hood et al., 2015) but effects vary with season of burn and fire intensity (Perrakis et al., 2011; Hood et al., 2016). Short-term reductions in tree growth (Busse et al., 2000; Collins et al., 2014) and temporary increases in the probability of mortality from bark beetles (Breece et al., 2008; Stark et al., 2013) may follow prescribed fire. Although bark beetle-associated mortality following prescribed fire is generally relatively low at endemic population levels (Fettig and McKelvey, 2014), prescribed fire applied during concurrent drought and beetle outbreak may render forests less resistant.

The Stanislaus-Tuolumne Experimental Forest (STEF; located on the Stanislaus National Forest) experienced elevated rates of tree mortality during California's most recent drought (Knapp et al. 2021), but mortality levels were somewhat lower than what was reported for the southern Sierra Nevada (Fettig et al., 2019; Restaino et al., 2019), where the drought was even more severe. While experimentally thinned treatments appeared to mitigate drought-related mortality, prescribed fire had more variable effects across species, adversely affecting pines but showing negligible effects for white fir (Knapp et al., 2021). Although the proximal agent of mortality was assumed to be bark beetles (Fettig et al., 2019), evidence relating bark beetle-associated

mortality to an individual tree's response to drought and treatments are lacking. The aims of this study were to (1) evaluate how thinning and prescribed fire treatments influenced drought resistance in terms of allocation to growth and defense and (2) determine whether drought resistance was related to bark beetle-associated mortality. Based on findings from Knapp et al. (2021), we expected that reduced competition following thinning would alleviate drought stress even after multiple years of severe drought, while prescribed fire would lessen drought resistance, especially when applied in stands with higher levels of competition. While we anticipated drought resistance to be negatively associated with bark beetle-associated mortality, it is also possible that growth and defense do not have similar relationships. During this recent drought, growth was shown to have inconsistent relationships with bark beetle-associated mortality across multiple species (Stephenson et al., 2019; Reed and Hood, 2021; Steel et al., 2021; Hood et al., 2022), and we expected the same in our study. Constitutive defenses that are present in species like sugar pine (*Pinus lambertiana* Douglas) may prove to be a more informative proxy for resistance to bark beetle-associated mortality than growth (Reed and Hood, 2021). The findings from this study can help elucidate mechanisms of bark beetle-associated mortality and inform land managers about potential treatments for promoting resistance to future disturbances.

2. Methods

2.1. Study area

Our study site consisted of a 100-ha mixed-conifer forest located within the STEF in the central Sierra Nevada of California (38°10'22"N, 120°00'00"W; Fig. 1). Stands at this site (elevation range between 1740 m and 1900 m) are composed of white fir (*Abies lowiana* [Gordon & Glend.] A. Murray bis), sugar pine, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), Jeffrey pine (*Pinus jeffreyi* Balf.), and incense-cedar (*Calocedrus decurrens* [Torr.] Florin) (USDA-NRCS, 2022). Climate at STEF is characterized as Mediterranean, with warm, dry summers and cool, wet winters. In the years preceding drought (2007 – 2011), average temperatures ranged from 0.7 to 3.6 °C in January to 18.4 – 21.1 °C in July. Annual precipitation ranged from 68.8 to 160.4 cm (PRISM climate group, 2021). Substantial departures from 30-year averages occurred during the extended drought, with above average temperatures and below average precipitation (Knapp et al., 2021). From 2012 to 2016, average January temperatures were over 50% higher (range = 1.5 – 7.5 °C), while July temperatures were similar to pre-drought conditions (range = 18.9 – 21.9 °C). Annual precipitation decreased by 21 to 47% (range = 36.7 – 126.0 cm) during the same time period, with the lowest Palmer Drought Severity Index (PDSI, -7.01) in California's recorded history occurring in 2014 (ncdc.noaa.gov/cag/stat ewide/time-series), indicating severe drought. Prior to fire exclusion, median fire return interval was 6 years (Knapp et al., 2013), with the last recorded fire occurring in 1889. A combination of selective logging in the 1920's that removed over 80% of the larger pines, and a lack of fire since 1889 resulted in a forest characterized by high densities of smaller-sized trees and a greater abundance of more shade-tolerant species (Knapp et al., 2013).

2.2. Treatments

The variable density thinning (VDT) study was initiated by the USDA Forest Service to restore stand structures more similar to conditions present prior to logging and fire suppression. In 2011, three different thinning treatments (unthinned, low variability, and high variability) were applied across 24 (4 ha) units (Knapp et al., 2017). The high variability thinning treatment left trees in groups of varying size and density, widely spaced individual trees, and small (0.04 to 0.2 ha) gaps, while the low variability thinning treatment produced relatively evenly spaced residual trees, with approximately 0.5-crown widths between

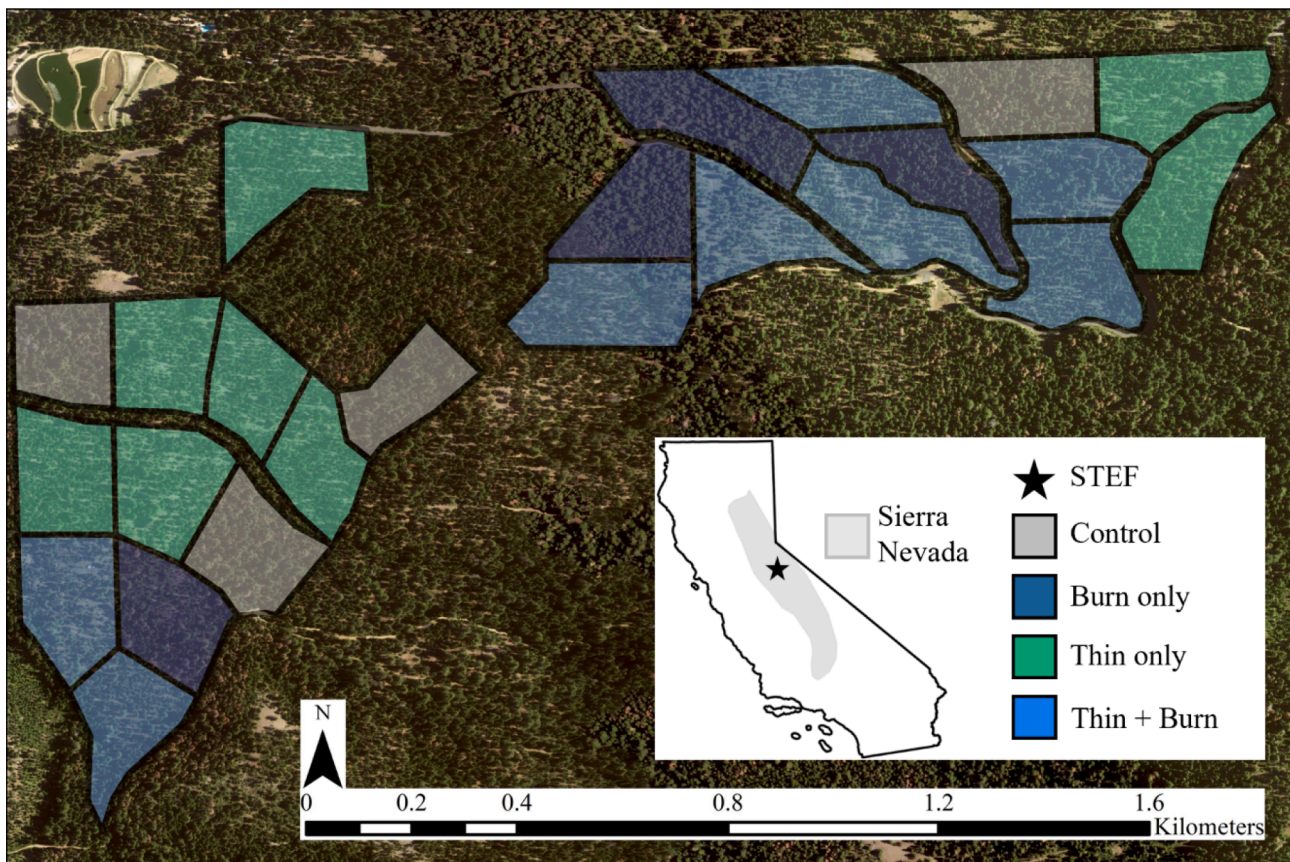


Fig. 1. Location of Stanislaus-Tuolumne Experimental Forest (STEF) in the central Sierra Nevada of California, USA, including delineation of unit boundaries and treatments. Thin treatments include both low and high variability thinning.

neighbors. For thinning, the “best” trees (largest trees and/or trees with the best crown form) were generally retained, with pines favored for retention over other species (e.g., incense-cedar and white fir) (Knapp et al., 2012, 2017).

In Fall of 2013, half of the units were burned with a low-intensity prescribed fire under moderate weather and fuel moisture conditions (see Knapp et al., 2017 for detailed prescribed fire prescription information). Thinned units contained similar tree density, basal area, size class distribution, and species composition but differed in the spatial arrangement of trees (Knapp et al., 2017, 2021). Thinned units were therefore grouped for the present study, resulting in four different treatments: unthinned-unburned (Control), burn only (Burn), thin only (Thin), and thinning followed by prescribed fire (Thin + Burn).

2.3. Data collection: Trees

To determine how drought resistance varied with treatments and between tree mortality outcomes, we sampled paired trees in 2017 to compare growth and defense characteristics between trees that died from bark beetle-associated mortality and trees that survived. To select subject trees within each unit, we randomly chose grid points from a pre-existing 30 m grid and conducted a 15 m radius search to select the nearest recently dead sugar pine and white fir. We defined “recently dead” as trees that exhibited characteristics of decay consistent with mortality within the last four years, including retention of intact dead needles, fine branches, and major limbs (Raphael and Morrison, 1987). Once we located a suitable tree, we removed enough bark to confirm bark beetle activity by identifying larval galleries of fir engraver (*Scolytus ventralis* [LeConte]) on white fir and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) on sugar pine. To control for other biotic agents of mortality, we excluded trees that showed signs of pathogens

not associated with fir engraver and mountain pine beetle (Paine et al., 1997). We also excluded trees that showed signs of abiotic agents of mortality such as mechanical damage, lightning scars, and severe fire injuries. When a tree satisfied these criteria, we paired it with a live intraspecific tree of similar size (≤ 7 cm difference in diameter at breast height [1.37 m aboveground]; DBH) and similar environmental conditions (≤ 40 m distance between trees). For each selected tree, we recorded species, status (dead or live), and DBH (cm). We repeated this process for all grid points until two pairs of each species were selected in each unit. While our target sample size was two pairs for each species in each unit (48 pairs for each species), a combination of low tree mortality and restrictive experimental design criteria led to reduced sampling in some units. In sum, 48 pairs of white fir and 39 pairs of sugar pine were selected (Appendix A).

2.4. Estimating tree-level competition

To evaluate how competition affects beetle host vulnerability to drought, we estimated the competitive environment of each subject tree in a nested 20 m fixed-radius plot. Although previous studies conducted in the Sierra Nevada used plot radii of 10 m to evaluate the influence of competition on tree vigor (Das et al., 2008, 2011), we extended all plot radii to 20 m to adequately represent competition in units where greater thinning intensity resulted in little to no competition within 10 m of a subject tree. With the subject tree as plot center, we recorded the species, status, DBH, and distance to competitor trees within each plot. Competitor trees with a DBH between 10 and 25 cm were included within a 5 m radius, trees with a DBH between 25 and 45 cm were included within a 10 m radius, and trees with a DBH ≥ 45 cm were included within a 20 m radius. Because of its strong correlation with growth across multiple species (Contreras et al., 2011), we used the

Hegyi index to estimate the competitive environment for each tree:

$$\text{Competition} = \sum_{j=1}^n \frac{DBH_j}{DBH_i(D_{ij} + 1)}$$

Where DBH_j is the DBH of the competitor tree, DBH_i is the DBH of the subject tree, and D_{ij} is the distance between the subject tree and competitor. This index estimates the weighted contribution of each competitor tree based on its relative size and distance from the subject tree (Biging and Dobbertin, 1992). To ensure that paired trees were in similar competitive environments, we compared competition between paired trees using a one-way ANOVA on log-transformed Hegyi index data. Paired live and dead trees were within the same treatment unit and competition did not vary between paired trees for white fir ($F_{1,96}$, $P = 0.990$) or sugar pine ($F_{1,78}$, $P = 0.816$).

2.5. Estimating tree vigor

To discern the effects of treatment on drought resistance, we conducted tree ring analyses for each subject tree. Using an increment borer, we extracted one 5 mm wide core from each live and dead tree at approximately breast height (1.37 m above ground) and allowed each core to dry prior to mounting them on wood blocks. Once mounted, we progressively sanded each core with an orbital sander using 80- to 600-grit sandpaper and then manually sanded with 800- to 1500-grit sandpaper. After processing, we scanned each core to create a high-resolution (1200 dpi) image. Each scanned image was imported into WinDendro¹ (Regent Instruments, Quebec, Canada), where we assigned annual ring boundaries and measured ring widths ($\pm 0.0001 \text{ cm y}^{-1}$). We created a cross-dated master chronology for all live trees of each species using ring width series in COFECHA (Holmes, 1983). Using this master chronology, we cross-dated the ring width series of each dead tree and estimated the year of mortality. We assumed the last full annual growth ring for each dead sample represented the year of mortality, but it is possible the actual year of mortality is later than reported due to mortality occurring prior to the initiation of radial growth, cessation of tree growth, or unaccounted absent tree rings. Based on these assumptions, we found that none of our trees died before the drought (2012). Outputs from COFECHA included series intercorrelation (site level similarities) and mean sensitivity (annual variability in ring width). Tree ring series for sugar pine had an intercorrelation of 0.464 and a mean sensitivity of 0.208, while white fir had an intercorrelation of 0.532 and a mean sensitivity of 0.198. Using these tree ring series, we calculated annual growth using the basal area increment (BAI; cm^2) for each tree from 2007 to 2016. BAI was used for growth because it would make our results comparable to previous drought resistance studies (Low et al., 2021; Vernon et al., 2018; Zald et al., 2022) and accounts for age and size differences across trees (Biondi and Qeadan, 2008).

In addition to growth, we quantified defense characteristics from sugar pine cores only, since white fir do not contain xylem resin ducts. Using scanned core images and ImageJ (Schneider et al., 2012), we estimated mean resin duct size (mm^2), resin duct production (number year^{-1}), total resin duct area ($\text{mm}^2 \text{ year}^{-1}$), resin duct density (number mm^{-2}), and relative resin duct area (%) (Appendix B), following methods presented in Hood et al. (2020). Preliminary analysis indicated high correlations among some resin duct measures (Appendix C). We therefore focused our analyses on each defense metric separately to avoid biased coefficient estimates and misleading significant relationships.

2.6. Estimating drought resistance

We defined drought resistance in live and dead sugar pine and white fir as the ability to maintain or increase growth during the years of drought relative to growth prior to drought, and expressed growth resistance as a ratio (Lloret et al., 2011):

$$\text{Growth resistance} = \frac{\text{Average growth}_{2012-2016}}{\text{Average growth}_{2007-2011}}$$

Our reference period pre-drought (2007 – 2011) was also used in Zald et al. (2022) to calculate treatment responses to drought and our drought period (2012 – 2016) was chosen based on low PDSI values beginning in 2012 and continuing through 2016. For sugar pine, we also defined defense resistance as the ability to maintain resin duct characteristics during drought years relative to pre-drought years and expressed defense resistance as a ratio analogous to growth. Since live trees have more years of growth than their dead counterparts, we avoided the potential for higher resistance ratios amongst live trees than dead ones by adjusting samples from each live tree to match the years of growth preceding mortality of its dead counterpart. For dead trees, the last year of growth/defense that was included in this measurement was the last full ring of tree growth.

2.7. Statistical analyses

To evaluate how treatments affected drought resistance and whether drought resistance varied with bark beetle-associated mortality, we fit species-specific generalized linear mixed-effects models using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2020). A nested random effect of treatment unit:pair was used to account for multiple live/dead paired subject trees within treatment replicates. To account for data that were positive, continuous, and highly skewed, we assumed a Gamma distribution with a log-link function. In our models, the response variables included growth resistance (white fir and sugar pine) and multiple defense resistance measures (sugar pine only) and independent variables included Hegyi index (a measure of competition used to represent thinning), burn treatment (unburned or burned), and tree status (live or dead). The Hegyi index was used instead of thinning treatment because an insufficient sample size for live and dead trees across units prevented us from analyzing the data at that scale. For each model, an interaction term was used between Hegyi index $\times$ status and burn $\times$ status to evaluate whether the relationship between drought resistance and mortality varied across treatments. When necessary, we also log-transformed Hegyi index values so that model residuals were normally distributed and homoscedastic. We removed one pair (sugar pine) from the dataset based on preliminary analysis showing that inclusion of the dead tree would have substantially biased our growth resistance model and result in misleading significant relationships. Because this individual tree appears to be an anomaly and not representative of our entire dataset, we report our growth resistance results excluding this sample. For several sugar pine, resin ducts were not present in the cores we extracted so defense resistance could not be quantified. In those cases, the pairs (6) were removed from the dataset and our results on defense resistance are reported excluding these samples.

3. Results

Based on Hegyi index, thinned plots had 38% less competition than plots in untreated stands. The application of prescribed fire had negligible effects on competition (Fig. 2). Based on cross-dated increment cores, tree mortality peaked in 2016 (38% for sugar pine and 63% for white fir), with mortality of sugar pine more evenly distributed across years than mortality of white fir (Fig. 3).

¹ The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

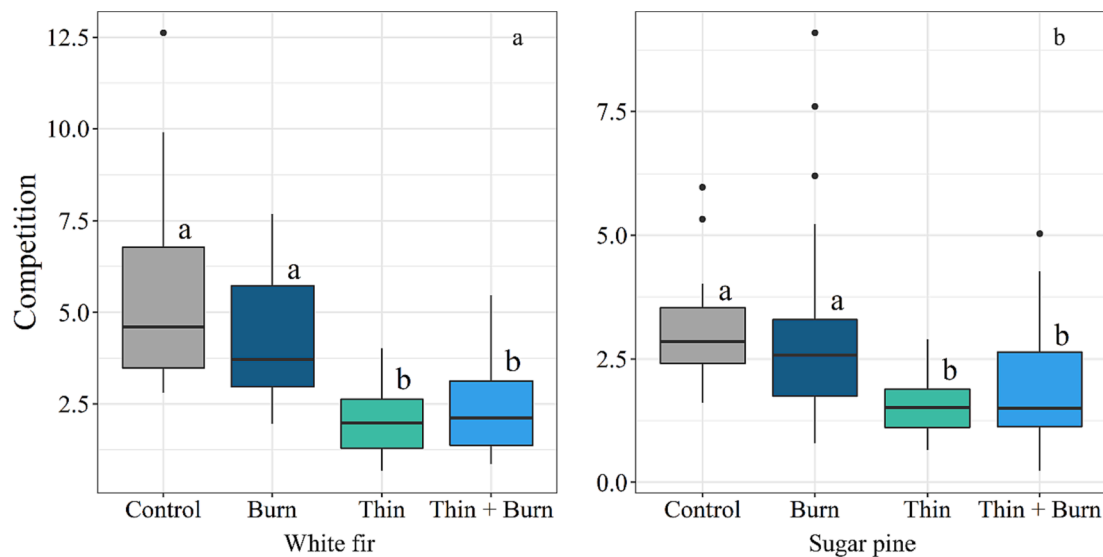


Fig. 2. Competition, as measured by the Hegyi index, surrounding paired white fir (a) and sugar pine (b) across treatments (note different scales for y-axis). Letters denote significant differences in competition among treatments for each species as determined by one-way ANOVA on log-transformed Hegyi index values.

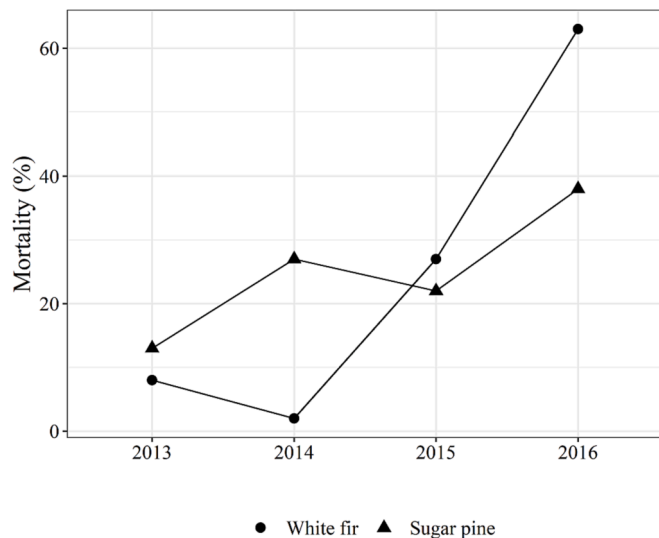


Fig. 3. Percentage of sampled dead white fir (circle) and sugar pine (triangle) trees by year of mortality based on last year of growth.

3.1. White fir growth and mortality

Median growth resistance of white fir was 12% higher in thinned units (1.12) than in unthinned units (0.99). When looking at competition as a surrogate for thinning, our model showed that growth resistance decreased as competition increased (Table 1 and Fig. 4a; $P < 0.001$). While median growth resistance was 6% higher in unburned units (1.12) than in burned units (1.05), this difference was not statistically significant ($P = 0.731$).

Median growth resistance of live white fir (1.10) was 3% higher than dead counterparts (1.06). This difference became more pronounced under higher levels of competition, where in unthinned stands live white fir showed 22% higher median growth resistance (1.06) than dead trees (0.83). When looking at competition as a surrogate for thinning, our model did find a significant interaction between competition and mortality ($P = 0.002$) which indicates that live white fir had greater growth resistance than dead counterparts especially at higher levels of competition (Fig. 4a). While live trees showed 6% lower median growth

resistance (1.01) than dead trees (1.07) in burned units and 10% higher median growth resistance (1.14) than dead trees (1.03) in unburned units, we did not detect a significant interaction between burn treatment and mortality ($P = 0.131$).

3.2. Sugar pine growth, defense, and mortality

Thinning and prescribed fire had varying effects on sugar pine growth and defense. Median growth resistance in thinned units (1.32) was 31% higher than unthinned units (0.91). However, when we looked at competition as a surrogate for thinning, our model did not detect a significant relationship between growth resistance and competition (Fig. 4b and Table 1; $P = 0.950$). Prescribed fire showed a similar trend to white fir, where median growth resistance in unburned units (1.10) was 3% higher than burned units (1.065), but the effect of prescribed fire was not significant ($P = 0.737$). However, our model showed that reduced competition and prescribed fire did have a positive impact on defense resistance (Fig. 5). Duct production ($P = 0.015$), duct density ($P = 0.001$), and relative duct area ($P = 0.026$) increased as competition decreased, and were also higher in units that were burned ($P = 0.005$, 0.003, 0.030, respectively).

Median growth resistance of live sugar pine (1.09) was 13% higher than dead counterparts (0.95), with our model indicating that growth resistance was positively related to survivorship (Fig. 4b and Table 1; $P = 0.003$). However, we did find an interaction between competition and mortality ($P = 0.042$), with live sugar pine showing a greater reduction in growth resistance as competition increased. Median duct size (1.15), duct production (1.25), total duct area (1.48), duct density (1.20), and relative duct area (1.35) for live trees were 11 to 27% higher than for dead trees (0.90, 1.00, 1.07, 1.07 and 1.05, respectively). We did find a significant interaction between defense resistance and mortality ($P = 0.004$ for duct density and $P = 0.021$ for relative duct area), showing that live trees had greater defenses than dead counterparts (31% for duct density and 24% for relative duct area) especially at higher levels of competition (Fig. 5). Not only did live sugar pine have greater defenses than dead trees, they also showed an increase in defenses as competition increased. While prescribed fire increased defense resistance, there was not an interaction between burn and mortality for any duct metric ($P = 0.539 - 0.817$).

Table 1

Generalized linear mixed-effects model inputs and outputs predicting growth and defense resistance metrics for white fir (WF; growth only) and sugar pine (SP; growth and defense). Defense resistance includes duct (D) size, production, total area, density, and relative (rel.) area. For status (live or dead) and burn (burned or unburned), reference levels live and burned were used in our outputs. Any log-transformed (L) variables are also indicated. Values in bold indicate significance based on an alpha level of 0.05.

Species	Response variable	Independent variables	Coefficient estimate	Standard error	p-value
WF	Growth	Hegyi index	-0.104	0.024	<0.001
		Status	-0.085	0.096	0.376
		Burn	-0.034	0.100	0.731
		Hegyi*Status	0.069	0.022	0.002
		Burn*Status	-0.135	0.089	0.131
SP	Growth	L(Hegyi index)	-0.023	0.112	0.836
		Status	0.372	0.123	0.003
		Burn	0.039	0.153	0.800
		L(Hegyi)*Status	-0.231	0.113	0.042
		Burn*Status	-0.197	0.130	0.130
SP	D. size	Hegyi index	0.006	0.064	0.920
		Status	0.050	0.198	0.800
		Burn	-0.026	0.200	0.895
		Hegyi*Status	0.058	0.066	0.380
		Burn*Status	-0.075	0.194	0.698
SP	D. production	Hegyi index	-0.186	0.077	0.015
		Status	0.085	0.238	0.720
		Burn	0.674	0.241	0.005
		Hegyi*Status	0.094	0.075	0.211
		Burn*Status	-0.097	0.242	0.689
SP	Total D. area	L(Hegyi index)	-0.311	0.172	0.072
		Status	0.255	0.223	0.252
		Burn	0.461	0.242	0.057
		L(Hegyi)*Status	0.100	0.188	0.595
		Burn*Status	-0.057	0.245	0.817
SP	D. density	Hegyi index	-0.254	0.074	0.001
		Status	-0.332	0.248	0.181
		Burn	0.651	0.221	0.003
		Hegyi*Status	0.236	0.081	0.004
		Burn*Status	0.153	0.249	0.539
SP	Rel. D. area	Hegyi index	-0.166	0.075	0.026
		Status	-0.162	0.252	0.522
		Burn	0.482	0.221	0.030
		Hegyi*Status	0.190	0.083	0.021
		Burn*Status	0.146	0.248	0.557

4. Discussion

Our study aimed to understand the effects of thinning and prescribed fire on growth and defense resistance and to determine whether these resistance metrics are related to bark beetle-associated mortality. Although previous research has shown that treatments can promote drought resistance in live trees (Thomas and Waring, 2015; Vernon et al., 2018; Low et al., 2021), comparing drought resistance between trees that survived bark beetle-associated mortality and those that died provides a better understanding of the physiological mechanisms that enable trees to resist multiple disturbances. This is the first study – to our knowledge – that attempts to explicitly link the relationship between a commonly-used quantification of drought resistance (Lloret et al., 2011; van Mantgem et al., 2020) and resistance to bark beetle-associated mortality across multiple species. We found that reducing competition can be beneficial for promoting growth resistance in white fir. We also found that prescribed fire had negligible impacts on growth resistance for both species but had positive impacts on defense resistance when defense characteristics could be quantified (i.e., species like sugar pine with resin ducts in the xylem). This finding suggests that prescribed fire

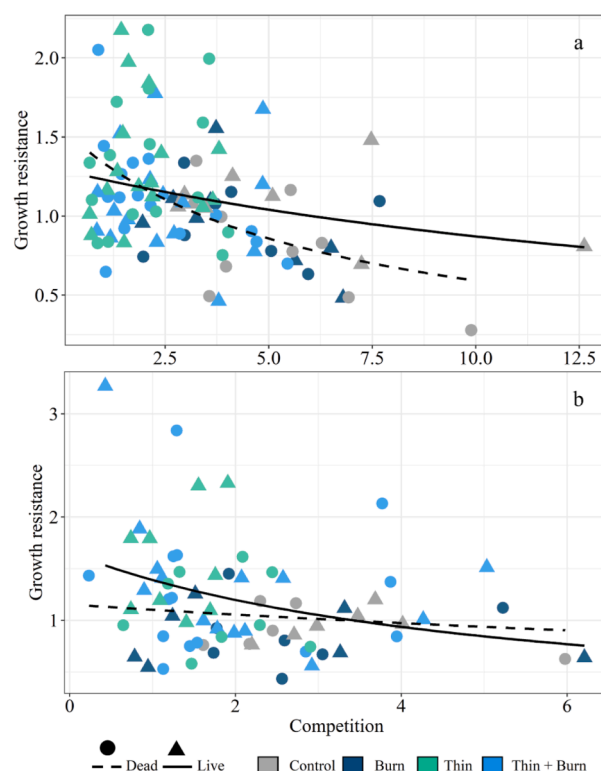


Fig. 4. Model response curves predicting growth resistance in white fir (a) and sugar pine (b). Competition was measured using the Hegyi index (note different scales for x- and y-axis). Shapes refer to live (triangle) and dead (circle) trees, while colors indicate treatment. Solid line indicates model output for growth resistance for live trees across a gradient of competition, while the dashed line is for dead trees.

treatments can provide the additional benefit of promoting defenses against bark beetles without the expense of maintaining tree growth during drought. Growth resistance was related to bark beetle-associated mortality for both species, while sugar pine also showed that defense metrics were related to drought vulnerability. The importance of defense systems in sugar pine becomes particularly important at higher levels of competition, where live trees appeared to invest more in defense than dead trees which may have enabled them to better survive bark beetle outbreak.

4.1. Treatments and growth resistance

We found that reduced competition improved growth resistance for white fir but had minimal impacts for sugar pine (Fig. 4). Thinning at our site significantly lowered competition for white fir (Fig. 2a), which may have increased soil water content and water uptake for residual trees (Feeney et al., 1998; Wallin et al., 2004). Increased resistance to drought following thinning has been observed at other sites and for other coniferous species (Vernon et al., 2018; Low et al., 2021; Zald et al., 2022). Thinning can improve physiological performance by alleviating water stress (Sala et al., 2005), which can increase drought resistance (Vernon et al., 2018; Low et al., 2021). Although competition was also significantly reduced for sugar pine (Fig. 2b), we did not find any relationship between competition and growth resistance. While Knapp et al. (2021) found that growth was related to competition, this relationship was more pronounced in other species such as white fir and incense-cedar. Agreement between our studies indicate differential responses to drought and treatment across species. Since species with constitutive defense systems, like sugar pine, may prioritize resources towards defenses instead of growth under periods of stress (Herms and Mattson,

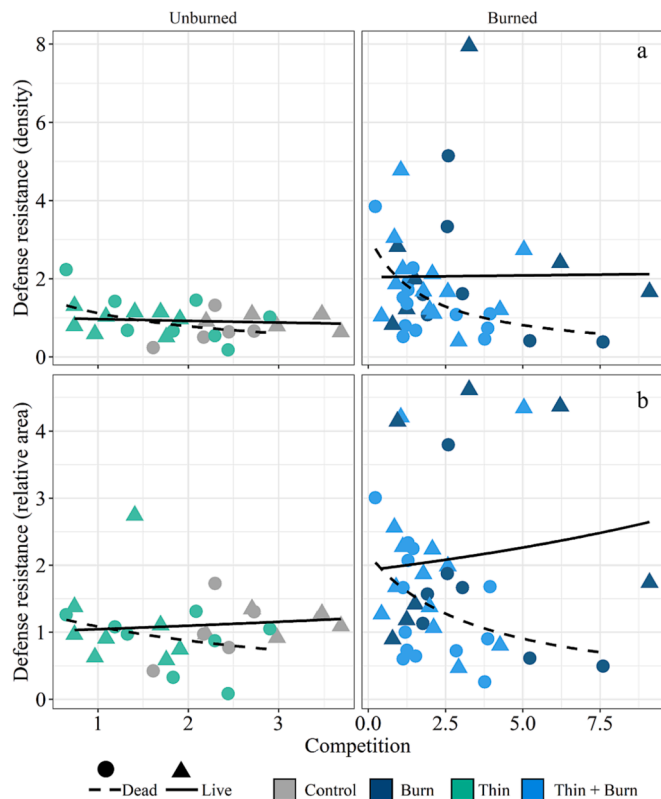


Fig. 5. Model response curves predicting defense resistance in sugar pine. While other defense traits were measured, we only included duct density (a) and relative duct area (b) because these had the strongest relationship with bark beetle-associated mortality (note different scales on x- and y-axis). Competition was measured using the Hegyi index. Shapes refer to live (triangle) and dead (circle) trees, while colors indicate treatment. Solid line indicates model output for defense resistance for live trees across a gradient of competition, while the dashed line is for dead trees.

1992), it is possible that the effects of competition on growth were muted due to this reallocation.

Our findings showed that prescribed fire alone had little impact on growth resistance for both species, regardless of competition. While low intensity fires can cause cambial injury, loss of roots, and reductions of non-structural carbohydrate concentrations (Stephens and Finney, 2002; Varner et al., 2009; Slack et al., 2016) that can contribute to declines in radial growth relative to trees that have not experienced burning, we did not observe these effects in our study. This finding was consistent with a similar study conducted in older mixed-conifer stands in the southern Sierra Nevada (Zald et al. 2022). The same VDT study (Knapp et al., 2021) found that pine BAI was less in burned units compared to unburned units, while burning showed little impact on white fir. However, Knapp et al. 2021 derived BAI from DBH measurements and cautioned that sloughing of charred bark in the years following prescribed fire would appear as reduced growth. Our BAI measurements were taken from tree cores, which is a more accurate measurement of growth. Therefore, our finding that prescribed fire alone has little impact on growth resistance appears more likely.

Similar to biotic agents that produce tree wounding (Hood and Sala, 2015), fire can induce a defensive response in trees (Lombardero et al., 2006). We found that sugar pine in prescribed fire units tended to have more resin ducts, higher resin duct density, and higher relative duct area. Low-severity fire can increase resin duct production (Hood et al., 2015) which may be particularly beneficial for improving tree defense. However, Hood et al. (2016) found thinning, rather than prescribed fire, stimulated defenses. This inconsistency may possibly be explained by the fall timing of prescribed fire at our site. Fuels are often drier in the

fall, and higher consumption can increase fire intensity (Knapp et al., 2009). If tree injury is a function of fire intensity, a greater defensive response might be observed. While these findings highlight how prescribed fire can be a tool specifically utilized to promote defensive capacity, the interactions between tree phenology, fire intensity, and timing of fire warrant more research.

Thinning alone can also increase resin duct characteristics (Hood et al., 2016), and our study found reductions in competition did increase duct production, duct density, and relative duct area. However, this relationship varied between dead and live sugar pine, with live sugar pine increasing defenses as competition increased. Prior to mortality, dead sugar pine showed lower vigor (i.e., growth resistance) than live trees (Fig. 4b) which may have limited their production of defenses especially under higher levels of competition (Herms and Mattson, 1992). Because live sugar pine had a stronger reduction in growth resistance as competition increased (i.e., significant Hegyi index $\times$ status), this could indicate that they prioritized resources towards defense systems which enabled them to withstand bark beetle-associated mortality.

4.2. Drought resistance and mortality

Limited resources during drought can lead to declines in tree health (Eamus et al., 2013), possibly predisposing trees to bark beetle selection or inhibiting the ability of trees to defend themselves against attack (Raffa et al., 2008). If trees that survived had more resources during drought to resist selection or beetle attack, then patterns of tree vigor may vary between trees that survived and those that died. We found this to be the case for both sugar pine and white fir, which is consistent with other studies that found short-term declines in growth rates prior to tree mortality (Kane and Kolb, 2014) and constitutive resin duct properties related to resistance (Kane and Kolb, 2010; Ferrenberg et al., 2014; Slack et al., 2021).

Our interpretation of how drought resistance relates to mortality has several caveats. Averaging over several years of drought may have limited our ability to detect any variation in trends related to mortality (Das et al., 2007; Kane and Kolb, 2014; Slack et al., 2021). We also assumed that the reference period we used represented “normal” conditions (Schwarz et al., 2020). Although reference periods can be based on years when the average drought stress is closest to zero (Stephenson et al., 2019), we chose the five years preceding drought to make our results comparable with other studies evaluating resistance during the same time period (Vernon et al., 2018; Low et al., 2021; Zald et al., 2022). While a more standardized approach to quantifying drought resistance has been proposed (Schwarz et al., 2020), these expressions of drought resistance are still intended to evaluate a single time point of drought (Lloret et al., 2011) and not the multi-year drought we analyzed. Attempting to modify resistance metrics that accommodate several years of drought was beyond the scope of our project and is a fruitful area for further investigation.

4.3. Management implications

With disturbances expected to increase in frequency and severity with climate change (Seidl et al., 2017), the relationships between resistance and mortality are important for understanding how we design treatments to reduce tree mortality. For gymnosperms, the ability to maintain pre-drought growth rates is critical for retaining the capacity to resist mortality during future drought events (DeSoto et al., 2020). Long-term growth patterns can also be an indicator of mortality to future fire events, with slower growth preceding fire increasing the likelihood of mortality (van Mantgem et al., 2020). Our observations of greater growth resistance in live sugar pine and white fir suggest that treatments which improve tree vigor can substantially increase the likelihood of survival to multiple disturbances. Our paired (live and dead) study design did not allow us to directly evaluate differences in mortality rates

across treatments, but previous work at our study site by Knapp et al. (2021) found that only 11% of trees in thinned units died during the drought, compared to 34% in adjacent untreated controls. Our findings complement this research by explaining the mechanisms behind differing rates of mortality. While our findings suggest that mortality can be mitigated with reduced competition and prescribed fire, interactions between site productivity and drought should be accounted for when contextualizing our results.

Prescribed fire is often employed to reduce fuels (Agee and Skinner, 2005), and we found that it also provided the benefit of stimulating resin defenses associated with resistance to bark beetle-associated mortality. The importance of chemically impairing and physically expelling bark beetles through these defensive mechanisms (Franceschi et al., 2005) cannot be understated. Resin ducts can remain functional for years, allowing trees to utilize resin defenses over the long-term (Hood and Sala, 2015) and enable them to survive future outbreak conditions. Our findings indicate that prescribed fire can produce these additional benefits, which are often not considered in traditional management objectives. While somewhat greater mortality occurred within all prescribed fire units (Knapp et al., 2021), mortality was especially pronounced in the unthinned units with greater competition. The relatively benign fuel moisture and weather conditions during prescribed burning at our site (Knapp et al., 2017), along with conservative ignition strategies to limit the chance of fire escape, may have decreased fire behavior such that burning alone had little impact on the high levels of competition that negatively impacted tree resistance to drought and bark beetles. The inability of prescribed fire alone to adequately alter structure in a highly productive site that has not experienced fire in over 100 years highlights the value of combining thinning treatments with prescribed fire to mitigate tree mortality. We found that both tree species are likely the most resistant to bark beetle-associated mortality in thinned and burned units. These findings suggest that reducing fuels with prescribed fire to moderate future wildfire behavior and promote resistance to bark beetles may not be conflicting objectives and can be particularly beneficial for improving the survivorship of multiple species

to compounding disturbances.

CRediT authorship contribution statement

Alexis A. Bernal: Methodology, Investigation, Formal analysis, Funding acquisition, Writing – original draft. **Jeffrey M. Kane:** Conceptualization, Methodology, Funding acquisition, Writing – original draft. **Eric E. Knapp:** Conceptualization, Funding acquisition, Writing – original draft. **Harold S.J. Zald:** Writing – original draft.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alexis Bernal reports financial support was provided by USDA Forest Service Pacific Southwest Research Station. Alexis Bernal reports financial support was provided by Joint Fire Science Program. Alexis Bernal reports financial support was provided by USDA Hispanic Serving Institute grant (CAMBIO program).

Data availability

Data will be made available on request.

Acknowledgements

We would like to thank two reviewers for their constructive feedback during the peer-review process. Funding for this project was provided by the United States Department of Agriculture Forest Service – Pacific Southwest Research Station [17-JV-11272167-019], Joint Fire Sciences Program [18-1-01-65], and the USDA Hispanic Serving Institute grant (CAMBIO program [2014-38422-22081]). Publication made possible in part by support from the UC Berkeley Library. Jessie Avitia, Alicia Abrego, Emily Hoeft, Austen Thibault, and Celeste Abbott assisted with field data collection. Bob Carlson provided logistical support for the project.

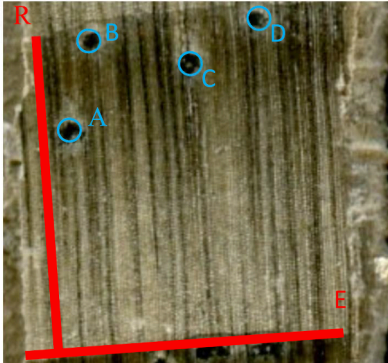
Appendix A:. Summary of paired white fir and sugar pine used for analyses, including number of sampled pairs in each treatment and tree size (DBH).

Species	Treatment	Sample pairs	Average dead DBH (range)	Average live DBH (range)
White fir	Control	8	35.0 (14.4–57.5)	34.5 (13.3–61.4)
	Burn	8	36.4 (23.7–50.3)	36.6 (22.7–51.8)
	Thin	16	47.5 (23.4–86.6)	48.5 (25.6–89.0)
	Thin + Burn	16	52.0 (30.3–71.9)	51.7 (29.3–72.5)
Sugar pine	Control	8	55.6 (28.3–94.1)	54.7 (27.2–90.8)
	Burn	8	57.4 (28.9–96.9)	58.6 (26.4–100.1)
	Thin	9	62.6 (25.00–102.3)	64.7 (25.0–101.4)
	Thin + Burn	14	55.2 (37.2–81.4)	56.2 (39.2–75.4)

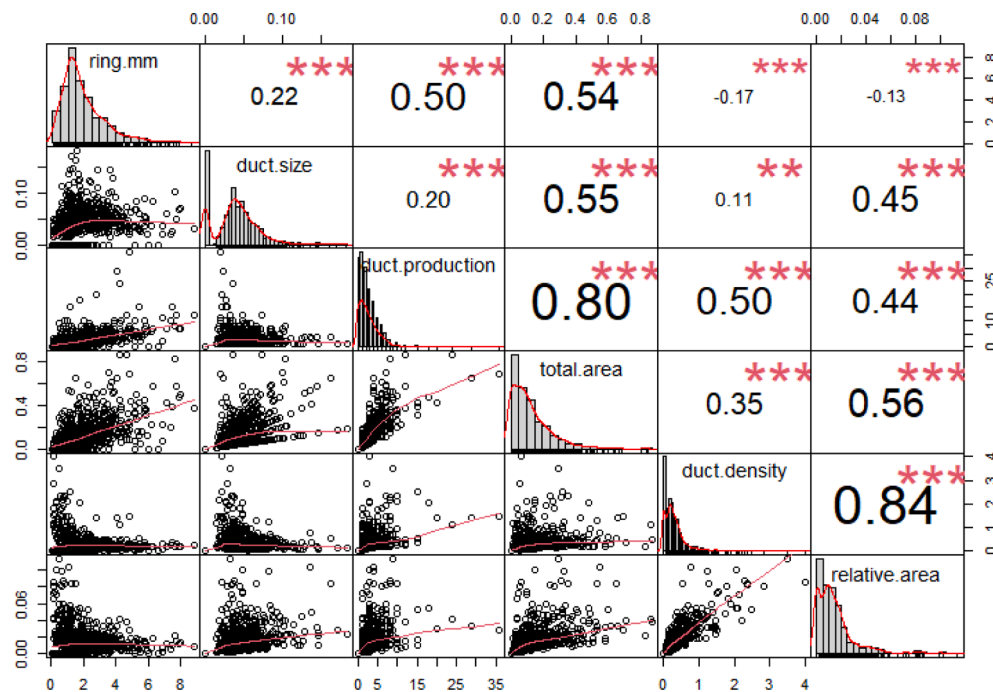
Appendix B:. Description of resin duct variables measured from sugar pine tree cores.

(continued on next page)

A = Ring area of duct A (mm²)
 B = Ring area of duct B (mm²)
 C = Ring area of duct C (mm²)
 D = Ring area of duct D (mm²)
 R = Ring width (mm)
 E = Core diameter (mm)
 R x E = Ring area (mm²)

Variable	Description	Formula	Example
 A = Ring area of duct A (mm²) B = Ring area of duct B (mm²) C = Ring area of duct C (mm²) D = Ring area of duct D (mm²) R = Ring width (mm) E = Core diameter (mm) R x E = Ring area (mm²)			
Variable	Description	Formula	Example
Average duct size (mm ²)	Average area of individual resin ducts/year	$\frac{\sum \text{resin duct area}}{\# \text{ resin ducts}}$	$\frac{A + B + C + D}{4}$
Duct production (no. year ⁻¹)	Total number of individual resin ducts/year	$\sum \text{of resin ducts}$	$1 + 1 + 1 + 1 = 4$
Total duct area (mm ⁻² year ⁻¹)	Sum of resin duct area	$\sum \text{resin duct area}$	$A + B + C + D$
Duct density (no. mm ⁻² year ⁻¹)	Total number of individual resin ducts /year divided by ring area	$\frac{\sum \text{of resin ducts}}{\text{ring area}}$	$\frac{1 + 1 + 1 + 1}{R \times E}$
Relative duct area (% annual ring)	Total resin duct area divided by ring area $\times 100$	$(\frac{\sum \text{resin duct area}}{\text{ring area}}) \times 100$	$(\frac{A + B + C + D}{R \times E}) \times 100$

Appendix C: Correlations between defense metrics including (from top to bottom), ring width, average resin duct size, resin duct production, total resin duct area, resin duct density, and relative duct area. The diagonal displays the distribution of each variable, the bottom diagonal displays the bivariate scatterplots and trendline (in red), and the top diagonal displays pearson's product moment correlation coefficient with significant correlations indicated for $p < 0.01$ () and $p < 0.001$ (***).**



References

- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211, 83–96. <https://doi.org/10.1016/j.foreco.2005.01.034>.
- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, 1–55. <https://doi.org/10.1890/ES15-00203.1>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience* 60, 602–613. <https://doi.org/10.1525/bio.2010.60.8.6>.
- Biging, G.S., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *For. Sci.* 38, 695–720. <https://doi.org/10.1093/forestscience/38.3.695>.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: Defining the biological trend from expected basal area increment. *Tree-Ring Res.* 64, 81–96. <https://doi.org/10.3959/2008-6.1>.
- Boone, C.K., Aukema, B.H., Bohlmann, J., Carroll, A.L., Raffa, K.F., 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Can. J. For. Res.* 41, 1174–1188. <https://doi.org/10.1139/x11-041>.
- Breece, C.R., Kolb, T.E., Dickson, B.G., McMillin, J.D., Clancy, K.M., 2008. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. *For. Ecol. Manage.* 255, 119–128. <https://doi.org/10.1016/j.foreco.2007.08.026>.
- Busse, M.D., Simon, S.A., Riegel, G.M., 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. *For. Sci.* 46, 258–268. <https://doi.org/10.1093/forestscience/46.2.258>.
- Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Cada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Cufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hereş, A.M., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanic, T., Linares, J.C., Mäkinen, H., Oberhuber, W., Papadopoulos, A., Rohner, B., Sangüesa-Barreda, G., Stojanovic, D.B., Suárez, M.L., Villalba, R., Martínez-Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nat. Commun.* 11, 1–9. <https://doi.org/10.1038/s41467-020-14300-5>.
- Eamus, D., Boulain, N., Cleverly, J., Breshears, D.D., 2013. Global change-type drought-induced tree mortality: Vapor pressure deficit is more important than temperature per se in causing decline in tree health. *Ecol. Evol.* 3, 2711–2729. <https://doi.org/10.1002/ece3.664>.
- Feeney, S.R., Kolb, T.E., Covington, W.W., Wagner, M.R., 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. *Can. J. For. Res.* 28, 1295–1306. <https://doi.org/10.1139/x98-103>.
- Ferrenberg, S., Kane, J.M., Mitton, J.B., 2014. Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia* 174, 1283–1292. <https://doi.org/10.1007/s00442-013-2841-2>.
- Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodka, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. *Glob. Chang. Biol.* 23, 1675–1690. <https://doi.org/10.1111/gcb.13535>.
- Collins, B.M., Das, A.J., Battles, J.J., Fry, D.L., Krasnow, K.D., 2014. Beyond reducing fire hazard: fuel treatment impacts on overstory tree survival. *Ecol. Appl.* 24, 1879–1886. <https://doi.org/10.1890/14-0971.1>.
- Contreras, M.A., Affleck, D., Chung, W., 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *For. Ecol. Manage.* 262, 1939–1949. <https://doi.org/10.1016/j.foreco.2011.08.031>.
- Das, A.J., Battles, J.J., Stephenson, N.L., Van Mantgem, P.J., 2007. The relationship between tree growth patterns and likelihood of mortality: A study of two tree species in the Sierra Nevada. *Can. J. For. Res.* 37, 580–597. <https://doi.org/10.1139/X06-262>.
- Das, A., Battles, J., Stephenson, N.L., van Mantgem, P.J., 2011. The contribution of competition to tree mortality in old-growth coniferous forests. *For. Ecol. Manage.* 261, 1203–1213. <https://doi.org/10.1016/j.foreco.2010.12.035>.
- Das, A., Battles, J., Van Mantgem, P.J., Stephenson, N.L., 2008. Spatial elements of mortality risk in old-growth forests. *Ecology* 89, 1744–1756. <https://doi.org/10.1890/07-0524.1>.
- DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Aakala, T., Amoroso, M.M., Bigler, C., Camarero, J.J., Cufar, K., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hereş, A.M., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Levanic, T., Linares, J.C., Mäkinen, H., Oberhuber, W., Papadopoulos, A., Rohner, B., Sangüesa-Barreda, G., Stojanovic, D.B., Suárez, M.L., Villalba, R., Martínez-Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nat. Commun.* 11, 1–9. <https://doi.org/10.1038/s41467-020-14300-5>.
- Eamus, D., Boulain, N., Cleverly, J., Breshears, D.D., 2013. Global change-type drought-induced tree mortality: Vapor pressure deficit is more important than temperature per se in causing decline in tree health. *Ecol. Evol.* 3, 2711–2729. <https://doi.org/10.1002/ece3.664>.
- Feeney, S.R., Kolb, T.E., Covington, W.W., Wagner, M.R., 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. *Can. J. For. Res.* 28, 1295–1306. <https://doi.org/10.1139/x98-103>.
- Ferrenberg, S., Kane, J.M., Mitton, J.B., 2014. Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia* 174, 1283–1292. <https://doi.org/10.1007/s00442-013-2841-2>.

- Fettig, C.J., Hayes, C.J., Jones, K.J., McKelvey, S.R., Mori, S.L., Smith, S.L., 2012. Thinning Jeffrey pine stands to reduce susceptibility to bark beetle infestations in California, U.S.A. *Agric. For. Entomol.* 14, 111–117. <https://doi.org/10.1111/j.1461-9563.2011.00543.x>.
- Fettig, C.J., McKelvey, S.R., 2014. Resiliency of an interior ponderosa pine forest to bark beetle infestations following fuel-reduction and forest-restoration treatments. *Forests* 5, 153–176. <https://doi.org/10.3390/f5010153>.
- Fettig, C.J., Mortenson, L.A., Bulaon, B.M., Foulk, P.B., 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *For. Ecol. Manage.* 432, 164–178. <https://doi.org/10.1016/j.foreco.2018.09.006>.
- Franceschi, V.R., Krokene, P., Christiansen, E., Krokling, T., 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytol.* 167, 353–376. <https://doi.org/10.1111/j.1469-8137.2005.01436.x>.
- Gaylord, M.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yezpe, E.A., Macalady, A.K., Pangle, R.E., McDowell, N.G., 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytol.* 198, 567–578. <https://doi.org/10.1111/nph.12174>.
- Goulden, M.L., Bales, R.C., 2019. California forest die-off linked to multi-year deep soil drying in 2012–2015 drought. *Nat. Geosci.* 12, 632–637. <https://doi.org/10.1038/s41561-019-0388-5>.
- Griffin, D., Anchukaitis, K.J., 2014. How unusual is the 2012–2014 California drought? *Geophys. Res. Lett.* 41, 9017–9023. <https://doi.org/10.1002/2014GL024333>.
- Herms, D.A., Mattson, W.J., 1992. The Dilemma of Plants: To Grow or Defend. *Q. Rev. Biol.* 67, 283–335. <https://doi.org/10.1086/417659>.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- Hood, S., Sala, A., 2015. Ponderosa pine resin defenses and growth: Metrics matter. *Tree Physiol.* 35, 1223–1235. <https://doi.org/10.1093/treephys/tpv098>.
- Hood, S., Sala, A., Heyerdahl, E.K., Boutin, M., Raffa, K.F., 2015. Low-severity fire increases tree defense against bark beetle attacks. *Ecology* 96, 1846–1855. <https://doi.org/10.1890/14-0487.1>.
- Hood, S.M., Baker, S., Sala, A., 2016. Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. *Ecol. Appl.* 26, 1984–2000. <https://doi.org/10.1002/eap.1363>.
- Hood, S.M., Reed, C.C., Kane, J.M., 2020. Axial resin duct quantification in tree rings: A functional defense trait. *MethodsX* 7, 101035. <https://doi.org/10.1016/j.mex.2020.101035>.
- Hood, S.M., Schaupp, W.C., Goheen, D.J., 2022. Radial thinning ineffective at increasing large sugar pine survival. *For. Ecol. Manage.* 520, 120351. <https://doi.org/10.1016/j.foreco.2022.120351>.
- Kane, J.M., Kolb, T.E., 2014. Short- and long-term growth characteristics associated with tree mortality in southwestern mixed-conifer forests. *Can. J. For. Res.* 44, 1227–1235. <https://doi.org/10.1139/cjfr-2014-0186>.
- Kane, J.M., Kolb, T.E., 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia* 164 (3), 601–609. <https://doi.org/10.1007/s00442-010-1683-4>.
- Knapp, E.E., Bernal, A.A., Kane, J.M., Fettig, C.J., North, M.P., 2021. Variable thinning and prescribed fire influence tree mortality and growth during and after a severe drought. *For. Ecol. Manage.* 479, 118595. <https://doi.org/10.1016/j.foreco.2020.118595>.
- Knapp, E.E., Estes, B.L., Skinner, C.N., Knapp, E.E., Estes, B.L., 2009. Ecological effects of prescribed fire season: A literature review and synthesis for managers. *Gen. Tech. Rep. PSW-GTR-224*. JFSP Synth. Reports 4, 80.
- Knapp, E.E., Lydersen, J.M., North, M.P., Collins, B.M., 2017. Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. *For. Ecol. Manage.* 406, 228–241. <https://doi.org/10.1016/j.foreco.2017.08.028>.
- Knapp, E., North, M., Benech, M., Estes, B., 2012. The variable-density thinning study at Stanislaus-Tuolumne experimental forest. In: North, M. (Ed.), *Managing Sierra Nevada Forests*. In: Gen. Tech. Rep., PSW-GTR-237. USDA For. Serv., Pacific Southwest Research, Station, Albany, CA, pp. 127–139.
- Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *For. Ecol. Manage.* 310, 903–914. <https://doi.org/10.1016/j.foreco.2013.09.041>.
- Kolb, T., Keefover-Ring, K., Burr, S.J., Hofstetter, R., Gaylord, M., Raffa, K.F., 2019. Drought-mediated changes in tree physiological processes weaken tree defenses to bark beetle attack. *J. Chem. Ecol.* 45, 888–900. <https://doi.org/10.1007/s10886-019-01105-0>.
- Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., Weed, A.S., 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *For. Ecol. Manage.* 380, 321–334. <https://doi.org/10.1016/j.foreco.2016.04.051>.
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>.
- Lombardero, M.J., Ayres, M.P., Ayres, B.D., 2006. Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. *For. Ecol. Manage.* 225, 349–358. <https://doi.org/10.1016/j.foreco.2006.01.010>.
- Low, K.E., Collins, B.M., Bernal, A., Sanders, J.E., Pastor, D., Manley, P., White, A.M., Stephens, S.L., 2021. Longer-term impacts of fuel reduction treatments on forest structure, fuels, and drought resistance in the Lake Tahoe Basin. *For. Ecol. Manage.* 479, 118609. <https://doi.org/10.1016/j.foreco.2020.118609>.
- Lydersen, J.M., North, M.P., Knapp, E.E., Collins, B.M., 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. *For. Ecol. Manage.* 304, 370–382. <https://doi.org/10.1016/j.foreco.2013.05.023>.
- Paine, T.D., Raffa, K.F., Harrington, T.C., 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annu. Rev. Entomol.* 42, 179–206. <https://doi.org/10.1146/annurev.ento.42.1.179>.
- Perrakis, D.D.B., Agee, J.K., 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. *Can. J. For. Res.* 36, 238–254. <https://doi.org/10.1139/x05-212>.
- Perrakis, D.D.B., Agee, J.K., Eglitis, A., 2011. Effects of prescribed burning on mortality and resin defenses in old growth ponderosa pine (Crater Lake. *Natural Areas Journal* 31 (1), 14–25.
- Varner, J.M., Putz, F.E., O'Brien, J.J., Kevin Hiers, J., Mitchell, R.J., Gordon, D.R., 2009. Post-fire tree stress and growth following smoldering duff fires. *For. Ecol. Manage.* 258, 2467–2474. <https://doi.org/10.1016/j.foreco.2009.08.028>.
- PRISM climate group, 2021. Climate data. <https://prism.oregonstate.edu/explorer/>. Accessed October 29, 2020.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58, 501–517. <https://doi.org/10.1641/B580607>.
- Raphael, M.G., Morrison, M.L., 1987. Decay and dynamics of snags in the Sierra Nevada, California. *For. Sci.* 33, 774–783. <https://doi.org/10.1093/forestscience/33.3.774>.
- Reed, C.C., Hood, S.M., 2021. Few generalizable patterns of tree-level mortality during extreme drought and concurrent bark beetle outbreaks. *Sci. Total Environ.* 750, 141306. <https://doi.org/10.1016/j.scitotenv.2020.141306>.
- Restaino, C., Young, D.J.N., Estes, B., Gross, S., Wuenschel, A., Meyer, M., Safford, H., 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. *Ecol. Appl.* 29, 1–14. <https://doi.org/10.1002/eap.1902>.
- Sala, A., Peters, G.D., McIntyre, L.R., Harrington, M.G., 2005. Physiological responses of ponderosa pine in western Montana to thinning, prescribed fire and burning season. *Tree Physiol.* 25, 339–348. <https://doi.org/10.1093/treephys/25.3.339>.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Schwarz, J., Skidaderis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying growth responses of trees to drought—a critique of commonly used resilience indices and recommendations for future studies. *Curr. For. Reports* 6, 185–200. <https://doi.org/10.1007/s40725-020-00119-2>.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trtschik, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Rey, C.P.O., 2017. Forest disturbances under climate change. *Nat. Clim. Chang.* 7, 395–402. <https://doi.org/10.1038/nclimate3303>.
- Slack, A.W., Kane, J.M., Knapp, E.E., 2021. Growth and defense inform large sugar pine (*Pinus lambertiana*) mortality in a fire-excluded forest of the central Sierra Nevada. *Trees* 35, 1053–1063. <https://doi.org/10.1007/s00468-021-02098-8>.
- Slack, A.W., Zeigler-Kichas, N.E., Kane, J.M., 2016. Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires. *For. Ecol. Manage.* 364, 130–138. <https://doi.org/10.1016/j.foreco.2016.01.014>.
- Stark, D.T., Wood, D.L., Storer, A.J., Stephens, S.L., 2013. Prescribed fire and mechanical thinning effects on bark beetle caused tree mortality in a mid-elevation Sierran mixed-conifer forest. *For. Ecol. Manage.* 306, 61–67. <https://doi.org/10.1016/j.foreco.2013.06.018>.
- Steel, Z.L., Goodwin, M.J., Meyer, M.D., Fricker, G.A., Zald, H.S.J., Hurteau, M.D., North, M.P., 2021. Do forest fuel reduction treatments confer resistance to beetle infestation and drought mortality? *Ecosphere* 12, e03344. <https://doi.org/10.1002/ecs2.3344>.
- Stephens, S.L., Finney, M.A., 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: Effects of crown damage and forest floor combustion. *For. Ecol. Manage.* 162, 261–271. [https://doi.org/10.1016/S0378-1127\(01\)00521-7](https://doi.org/10.1016/S0378-1127(01)00521-7).
- Stephenson, N.L., Das, A.J., Ampersee, N.J., Bulaon, B.M., Yee, J.L., Edwards, D., 2019. Which trees die during drought? The key role of insect host-tree selection. *J. Ecol.* 107 (5), 2383–2401. <https://doi.org/10.1111/1365-2745.13176>.
- R Core Team, 2020. R: A language and environment for statistical computing.
- Thomas, Z., Waring, K.M., 2015. Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in Northern New Mexico. *USA. For. Sci.* 61, 93–104. <https://doi.org/10.5849/forsci.13-085>.
- USDA Forest Service California Climate Hub, 2017. Drought and Tree Mortality in the Pacific Southwest Region. *Sci. Manag. Symp. - Lessons Learn. From Extrem. Drought Tree Mortal. Sierra Nevada How Can Past Events Inf. Our Approach Forward?* 1–14.
- USDA-NRCS, 2022. The PLANTS Database. <http://plants.usda.gov> (Accessed November 14, 2022).
- van Mantgem, P.J., Falk, D.A., Williams, E.C., Das, A.J., Stephenson, N.L., 2020. The influence of pre-fire growth patterns on post-fire tree mortality for common conifers in western US parks. *Int. J. Wildl. Fire* 29, 513–518. <https://doi.org/10.1071/WF19020>.
- van Mantgem, P.J., Stephenson, N.L., 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecol. Lett.* 10 (10), 909–916. <https://doi.org/10.1111/j.1461-0248.2007.01080.x>.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323, 521–524. <https://doi.org/10.1126/science.1165000>.
- Vernon, M.J., Sherriff, R.L., van Mantgem, P., Kane, J.M., 2018. Thinning, tree-growth, and resistance to multi-year drought in a mixed-conifer forest of northern California. *For. Ecol. Manage.* 422, 190–198. <https://doi.org/10.1016/j.foreco.2018.03.043>.

- Wallin, K.F., Kolb, T.E., Skov, K.R., Wagner, M.R., 2004. Seven-year results of thinning and burning restoration treatments on old ponderosa pines at the Gus Pearson Natural Area. *Restor. Ecol.* 12, 239–247. <https://doi.org/10.1111/j.1061-2971.2004.00278.x>.
- Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., Lloret, F., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecol. Lett.* 20 (1), 78–86. <https://doi.org/10.1111/ele.12711>.
- Zald, H.S.J., Callahan, C.C., Hurteau, M.D., Goodwin, M.J., North, M.P., 2022. Tree growth responses to extreme drought after mechanical thinning and prescribed fire in a Sierra Nevada mixed-conifer forest, USA. *For. Ecol. Manage.* 510, 120107. <https://doi.org/10.1016/j.foreco.2022.120107>.