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ORIGINAL ARTICLE

Growth and defense inform large sugar pine (*Pinus lambertiana*) mortality in a fire-excluded forest of the central Sierra Nevada

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Abstract

Key message **Large sugar pine mortality was associated with recent growth and defense measures.**

Abstract Many old-growth pine forests across the western United States have encountered widespread and concerning increases in tree mortality attributed to increased competition and reduced vigor associated with prolonged fire exclusion that can make trees more vulnerable to bark beetles. We investigated the importance of growth and resin duct defense on recent mortality of large sugar pine (*Pinus lambertiana*) in a fire-excluded, mixed-conifer forest of the Sierra Nevada, in California, USA. Growth and defense were measured from tree rings for 33 pairs of live and dead sugar pine. The 10-year trend in basal area increment prior to sampling declined by 1.78 cm^2 $year^{-1}$ in sugar pine that died and increased by 0.34 cm^2 $year^{-1}$ in paired live sugar pine. The 10-year trend in resin duct total area showed declines of 0.0154 mm^2 $year^{-1}$ in trees that died and increases of 0.0068 mm^2 $year^{-1}$ in trees that survived. The most informative models of large sugar pine mortality included measures of both growth and defense. The top model included the trends of basal area increment and resin duct total area 10 years before mortality, and growth variability 5 years before mortality. In general, trends and variability in growth and defense over shorter time windows (< 10 years) were more informative than average measures or longer time windows. The results from our study suggest treatments that result in neutral to positive trends in allocation to growth and defense may contribute to conditions that reduce probability of mortality in the future.

Keywords Bark beetles · Basal area increment · Dendrochronology · Logistic regression · Resin ducts · Competition · Tree mortality

Introduction

In recent decades, elevated temperatures have contributed to increased background mortality rates (van Mantgem et al. 2009) and large-scale die-off events in many forest ecosystems (Allen et al. 2010; Smith et al. 2015; Young et al. 2017). In the western United States, many old-growth pine stands also experience higher mortality where structure and composition have been dramatically altered by fire exclusion. Historically, high-frequency and low-intensity fire regimes once maintained more open stands, but in the absence of fire, many stands have become denser with a higher proportion of shade tolerant species (Naficy et al. 2010; Collins et al. 2011; Knapp et al. 2013; McIntyre et al. 2015). As a result, older and larger trees are often more prone to mortality than in the past due to pathogen and insect outbreaks, drought, and increased competition (Kolb et al. 2007; Bennett et al. 2015). Fire-excluded forests are sometimes more susceptible to large-scale mortality events because increased competition can place added stress on individual trees (Savage 1997; Allen 2007). The combination of greater competition and the effects of climate change could predispose trees and exacerbate tree mortality trends (Miller and Urban 1999; Battles et al. 2008; Young et al. 2017).

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Mechanisms that lead to tree mortality are often difficult to identify because multiple interacting factors may occur over the lifespan of a tree (Waring 1987; Manion 1991). Tree growth is a common measure used to retrospectively assess tree vigor over many years and slower growth preceding mortality has been a robust indicator in numerous species (Cailleret et al. 2017). While annual growth rate has often been associated with tree mortality, other growth patterns may provide a better early warning signal of mortality (Cailleret et al. 2019). Negative growth trends (i.e., the slope of growth over time) have improved the predictive capability of growth-dependent mortality models (Bigler and Bugmann 2003; Hanna and Kulakowski 2012; Kane and Kolb 2014). Additionally, trees that had higher year-to-year growth variability (i.e., more sensitive; Ogle et al. 2000; Kane and Kolb 2014; Cailleret et al. 2019) or more abrupt growth declines (i.e., substantial decreases in growth from 1 year to the next; Pedersen, 1998; Das et al., 2007) had a higher probability of mortality. Previous research has also found that the length of time analyzed matters. Some studies indicated that tree mortality was related to growth characteristics during shorter ($\leq$ 10 years) time windows (Ogle et al. 2000; Bigler and Bugmann 2004; Hanna and Kulakowski 2012), while others have associated tree mortality to longer ($\geq$ 10 y) time windows (Pedersen 1998; Bigler and Bugmann 2003; Das et al. 2007), or a combination of short- and long-term time windows (Kane and Kolb 2014).

Defense structures, such as resin ducts, have also been linked to tree health (Paine et al. 1997) and their presence in tree rings offer a retrospective assessment of potential tree defense over time (Kane and Kolb 2010). Vertical and radial resin ducts produced in the secondary xylem contain parenchyma cells within duct walls that synthesize oleoresins to chemically impair, isolate, and expel insects and pathogens (Franceschi et al. 2005). Resin ducts also create an extensive network that stores and transports resin to the site of bark beetle attack. The importance of resin duct defenses in reducing susceptibility to bark beetle attack and subsequent mortality has been demonstrated in a wide range of pine species, including ponderosa pine (*Pinus ponderosa*; Hood et al. 2015; Kane and Kolb 2010), pinyon pine (*P. edulis*; Gaylord et al. 2013), limber pine (*P. flexilis*), and lodgepole pine (*P. contorta* var. *latifolia*; Ferrenberg et al. 2014).

Old-growth forests are rare across most western US landscapes and the persistence of these ecosystems is of great concern to land managers (Kolb et al. 2007). Older and larger trees are highly valued for many ecological services, including critical wildlife habitat, long-term carbon sequestration, and ecosystem resiliency. Past logging practices and numerous environmental changes have contributed to underrepresentation of large trees in many landscapes (Kolb et al. 2007; Lutz et al. 2009; Knapp et al. 2013). For these reasons, there is substantial interest in preserving remnant old-growth stands and restoring previously impacted forests.

The main objective of our study was to determine the relative importance of growth and defense on the probability of mortality for large sugar pine in a fire-excluded, mixed-conifer forest of the central Sierra Nevada. The association between growth and sugar pine mortality has been relatively well studied (Das et al. 2007; Das and Stephenson 2015; Nesmith et al. 2015), but we are unaware of research examining the role of defense or comparing the relative importance of growth and defense and their relationship with sugar pine mortality. Specifically, we address the following research questions; (1) what are the pre-mortality differences in growth and defense between sugar pines that lived and those that died? and (2) what variables and time frames of growth and defense are most strongly associated with the probability of sugar pine mortality? By discerning the relative importance of these specific factors, managers interested in protecting large pine and restoring old-growth forests will be better equipped to develop effective management strategies.

Materials and methods

Study area

The study site covered about 55 ha of mid-elevation (1585–1890 m), mixed-conifer forest in the Stanislaus-Tuolumne Experimental Forest (38° 10' N, 120° 00' W) near Pinecrest, California, USA. Climate at the study site consists of warm dry summers and cold wet winters, with a majority of precipitation falling during the winter months, about half as snow. During the 50 years prior to and including the year of sampling, air temperature ranged from −25 to 35 °C with an annual average of 8.6 °C, and precipitation ranged from 364 to 2202 mm with an annual average of 1146 mm per year (PRISM Climate Group 2015). Subject sugar pine trees were located on north to northwest aspects with slopes ranging from 2° to 18°. Soils, formed from granite and weathered tuff breccia, were deep, well-drained loams to gravelly loams of the Wintoner-Inville families complex.

The historical fire regime of the Stanislaus-Tuolumne Experimental Forest had a median return interval of 6 years, but the stand has not experienced a fire since 1889 (Knapp et al. 2013). In the absence of fire, more shade-tolerant white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) have increased in abundance with proportionally less sugar pine, ponderosa pine, and Jeffrey pine (*P. jeffreyi*) (Knapp et al. 2013). The study area was mostly unlogged prior to 2012, when a thinning treatment was applied to approximately 80% of the study area that mostly removed smaller diameter trees and retained larger overstory trees.

A few old cut stumps existed prior to the recent thinning treatment, likely a result of localized sanitation salvage that removed dead and dying trees to reduce the population and spread of bark beetles. At the time of the study, mortality in the largest diameter classes was relatively low, with no evidence of recent major bark beetle outbreaks.

Field data collection

All available large standing dead sugar pine (> 50 cm diameter at breast height, DBH) within the study site were assessed in the summer of 2014. Any dead tree that produced a viable 12-mm diameter core at breast height with an increment borer were included in our study ($n = 33$) and paired with the a similar-sized (DBH ± 5 cm) live tree within 150 m (average distance of 58.2 m). Cores were extracted from live trees in the same manner as the dead trees. Live and dead trees ranged from 52 to 168 cm DBH (Fig. 1). Although we did not age any subject sugar pine because most cores did not extend to the pith, the number of rings captured in our cores showed that all sugar pines were at least 100 years old. The oldest trees were over 300 years old with a few cores containing more than 450 rings. The paired design limited differences in soils, topographic features, and other microsite conditions. Average total competition (inter- and intra-specific competition) Hegyi index values were 1.6 and 1.5 for live and dead sampled trees, respectively. These and all other measures of competition examined (i.e. basal area and tree density) did not significantly differ between live and dead trees ($p > 0.26$), likely due to the close proximity and similar dbh of the paired live and dead sugar pine. Thus, competition measures were not considered in subsequent model development and analyses. We measured DBH and bark thickness for all live and dead subject sugar pine. All dead sugar pine showed at least one sign or symptom of mountain pine beetle (*Dendroctonus ponderosae*) activity, including exit holes, galleries inside the bark, and associated fungal species (e.g., *Ophiostoma* spp., *Cryptoporus volvatus*). Eight of the sampled dead sugar pine also contained rhizomorphs at the base of the tree, indicating the presence of *Armillaria* spp. root disease. We presumed that the sampled trees ultimately died as a result of bark beetle attack, with root disease also contributing to mortality in a subset of these trees. However, we are unable to definitively assign the actual cause and mechanism of mortality.

Growth and defense measures

All tree cores were mounted and progressively sanded with 80- to 600-grit sand paper, then scanned to create a high-resolution (1200 dpi) image. Each image was analyzed in the program WinDendro (Regent Instruments Inc. 2014), where annual ring boundaries were assigned and total ring width (mm year^{-1}) was measured (Fig. 2). All cores were visually cross-dated and we used COFECHA (Grissino-Mayer 2001) to assess potential errors in assigning years to annual rings and to determine the last year of growth for all dead trees. Individual series were compared to a master chronology that was constructed from all subject trees in this study and an additional 70 live sugar pine from another study (Slack et al. 2017). The chronology for all 66 sugar pine trees had a mean sensitivity of 0.174, a measure of year-to-year variability in the chronology, and a series intercorrelation of 0.479, a measure of the stand-level signal. Based on cross-dating with the master chronology, the last year of growth (i.e., presumed year of death) in all dead sugar pine was between 1990 and 2013, with 29 of 33 trees dying between 2000 and 2012. Two of the sampled trees died in 2013, 1 year after the thinning treatment, but were included because the

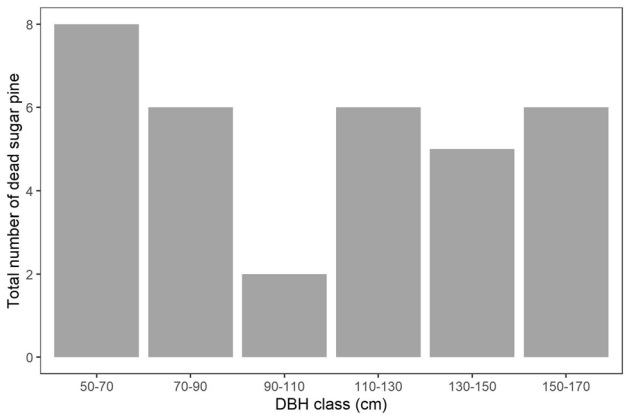

Fig. 1 Distribution of diameter at breast height (DBH) of dead sugar pine, which dictated the sampling for dead and live pairs. DBH ranged from 52 to 168 cm for all subject sugar pine, and live sugar pine followed a similar distribution

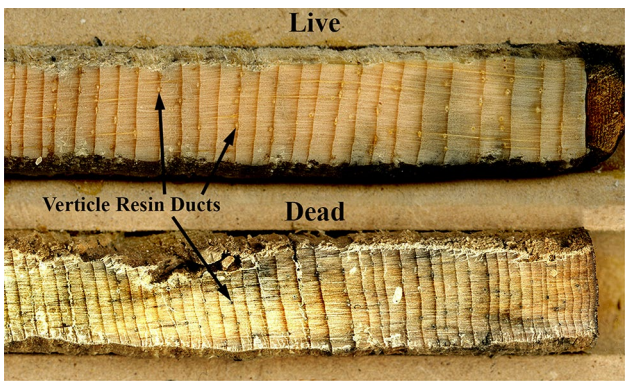

Fig. 2 A high-resolution photo of increment cores from a pair of live and dead sugar pine. Photos such as this were used to measure annual ring width and vertical resin ducts to quantify sugar pine growth and defense

thinning treatment likely had a minimal impact on growth and defense measures and they were paired with live trees that were also within thinned treatments.

Basal area increment (BAI; $cm^2\ year^{-1}$) was calculated (Eq. 1) for all 33 live and dead tree pairs over a 50-year period preceding mortality of the dead sugar pine. We used BAI as a measure of sugar pine growth to reduce the potential impacts of age- or size-related growth trends while still capturing suppression or release events that may be related to changes in climate or competition (Biondi and Qeadan 2008; Speer 2010).

$$\mathrm{BAI}_t = \pi\left(R^2 - r^2\right). \quad (1)$$

BAI_t was growth for year t, R was the outer radius, and r was the inner radius. This equation assumed that annual rings were geometrically circular and had a constant ring width within a year. The radius for each ring was determined by progressively subtracting annual ring widths from the diameter inside bark (DBH – 2 × bark thickness).

Sugar pine defense structures were estimated through measurements of vertical resin ducts within each annual tree ring over a 50-year period for all live and dead tree pairs sampled. Resin ducts were identified and measured from high resolution images of each core using the program ImageJ (Rasband 2014; Fig. 2). Resin duct size ($mm^2\ year^{-1}$) was measured as the average area of all resin ducts that were produced within an annual ring and resin duct total area ($mm^2\ year^{-1}$) was measured as the sum of all individual resin duct areas within an annual ring. When an annual ring did not have any resin ducts, resin duct size was not included but resin duct area was assigned a zero value. We also evaluated other resin duct measures, but found production (i.e. resin duct count per year), density, and relative area to be less informative or collinear with other measures.

In addition to average measures of sugar pine growth and defense, we also calculated measures of other temporal patterns. Year-to-year variability was determined by calculating the coefficient of variation for BAI and resin duct total area, representing the relative sensitivity in growth and defense for each time window examined. Trends were determined by calculating the slope of the relationship between the proxy measures of vigor (i.e., growth and defense) and time. For each pair of live and dead sugar pine, the 50 years before the last year of growth in the dead tree was analyzed to allow comparison of short-term (5- and 10-year) and long-term (25- and 50-year) time windows. Abrupt growth declines were defined as a BAI ≤ 50 % of the BAI from the previous year (Das et al. 2007), and the number of abrupt declines was counted for each tree over the 50-year time frame only. Preliminary analysis examining 50-year average growth and defense showed that BAI was not sufficiently correlated with resin duct size ($r = 0.08$, $p = 0.51$) or resin duct total area ($r = 0.36$, $p = 0.003$) to raise concerns of multicollinearity among these growth and defense measures.

Statistical analyses

All statistical analyses were performed in the program R (R Development Core Team 2018). We used paired t tests to examine the differences in growth and defense measures between live and dead sugar pine (question 1). When normality or equal variance assumptions were violated, we analyzed differences between live and dead sugar pine using the non-parametric Wilcoxon signed-rank test. The results from this analysis were also used to inform the inclusion of variables in building candidate mortality models (question 2).

Logistic regression was used to examine which variables of sugar pine growth and defense were most-strongly associated with mortality (question 2). This statistical analysis estimated the probability of mortality based on one or more predictor variables using the standard logistic function (Eq. 2).

$$P_m = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_m x_m)}}. \quad (2)$$

P_m was the probability of mortality, β_0 was the intercept estimate, and β_1 was the coefficient estimate for variable 1 (x_1). Logistic regression models were developed and analyzed using the package *glm2* (Marschner 2011).

Growth and defense variables included in candidate models were selected by comparing single variable models using Akaike's information criterion (AIC). Within each growth and defense variable (average, trend, variability), four time windows (5- 10-, 25-, 50-year) were compared and the predictor with the lowest AIC was included in the suite of candidate multivariate models. Each multivariate model was then verified for multicollinearity using the variance inflation factor (VIF), which describes how much of the variance is explained by including the ith variable with all other independent variables (O'brien 2007). It has been suggested that multicollinearity becomes severe when VIF exceeds 10 (Neter et al. 1996), however, other research has shown that multicollinearity can be problematic when VIF is as low as 2 (Graham 2003). To be conservative we only considered models with variables that had a VIF < 2.

Models were then created using all possible combinations of the subset of predictor variables selected using the *glmulti* package. We included DBH as a covariate in all sugar pine mortality models to account for the potential influence of tree size on growth and defense. The top model was selected using Akaike's information criterion with a correction factor (AICc) to better estimate model performance when limited by a small sample size. Meaningful differences between models were indicated by Δ AICc values greater than 2 (Burnham and Anderson 1998). We assessed and reported

all models with a Δ AICc less than 2 from the top model, and included comparison models with measures of growth or defense only.

To provide an estimate of model accuracy, we calculated the area under the receiver operating characteristic curve (ROC). In addition, each model was validated internally by calculating the percentage of correctly classified trees. We calculated the standardized coefficients (Eq. 3) post hoc for each variable in the top model to provide an estimate of the relative strength each variable has on the probability of large sugar pine mortality.

$$\beta_{s1} = \beta_1 \times \frac{s_1}{s_y}. \quad (3)$$

β_{s1} is the standardized coefficient for variable 1, β_1 is the unstandardized coefficient estimate for variable 1, s_1 is the standard deviation for variable 1, and s_y is the standard deviation for the response variable.

Results

Differences between live and dead sugar pine

Average BAI between trees that lived and trees that died did not differ during any time windows that ended in the last year of growth for the tree that died (Table 1). Interestingly, average growth between 10 and 50 years before tree death (i.e. excluding the 10 most recent years before tree death) was 25 % higher in trees that died than in trees that survived ($p = 0.0302$, Fig. 3). The greatest difference in average growth occurred between 45 and 50 years before tree death, when average growth in trees that died was 28 % higher than in trees that survived ($p = 0.0111$).

The growth trend (slope of growth over time) was on average negative for trees that died and positive for trees that lived during the 5, 10, and 25 years before tree death. The greatest difference in growth trend occurred during the 10-year time window when trees that died decreased growth by 1.78 $cm^2\ y^{-1}$ and trees that lived increased in growth by 0.34 $cm^2\ year^{-1}$ ($p < 0.0001$; Table 1; Fig. 3). The coefficient of variation in growth for trees that died was greater than trees that lived during the 5-year time window ($p = 0.0045$) and 10-year time window ($p = 0.0082$). Sugar pine that died also had more abrupt growth declines than sugar pine that lived in the 50 years before mortality ($p = 0.0179$). An average of 19 abrupt growth declines were found in sugar pine that died, and only 8 abrupt declines in sugar pine that lived.

Sugar pine that lived sustained allocation toward resin defenses compared to those that died. In the 5 years prior to mortality, 29 % less resin duct total area was found in trees that died ($p = 0.0276$; Table 2; Fig. 4). In general, the trend

Table 1 Growth characteristics by time window for live and dead sugar pine

	Live	Dead	*p* value
5-year time window			
Average	37.95 (3.22)	33.86 (3.66)	0.401
Trend	1.09 (0.65)	− 0.86 (0.56)	0.037*[W]
COV	0.17 (0.01)	0.23 (0.02)	0.005*
10-year time window			
Average	37.02 (3.03)	38.38 (4.14)	0.792
Trend	0.34 (0.23)	− 1.78 (0.49)	< 0.001*[W]
COV	0.21 (0.02)	0.28 (0.03)	0.008*[W]
25-year time window			
Average	34.87 (2.66)	39.97 (3.89)	0.279
Trend	0.34 (0.10)	− 0.18 (0.15)	0.016*[W]
COV	0.26 (0.02)	0.29 (0.02)	0.070
50-year time window			
Average	33.48 (2.38)	40.34 (3.69)	0.081
Trend	0.11 (0.06)	− 0.06 (0.08)	0.082
COV	0.28 (0.02)	0.29 (0.02)	0.688
Abrupt declines	0.24 (0.11)	0.58 (0.12)	0.018*[W]

Growth was measured as basal area increment ($cm^2\ year^{-1}$). Characteristics consisted of average, trend (slope of growth over time), growth variability (coefficient of variation; COV), and number of abrupt growth declines (50-year time window only). Values in parenthesis are standard error

p value is the results from paired *t* tests or Wilcoxon signed-rank tests, and significant differences between sugar pine that lived and died are highlighted by an asterisk

[W]Differences between live and dead sugar pine were tested using Wilcoxon signed-rank test

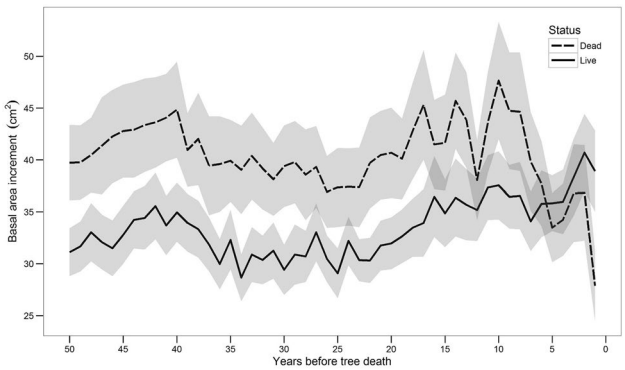

Fig. 3 Average basal area increment for dead (dashed) and live (solid) sugar pine 50 years prior to mortality of dead sugar pine. Dead sugar pine experienced steep declines in growth 10 years before mortality, while live sugar pine concurrently increased in growth. The earliest dead sugar pine died in 1991 and 73 % of trees died between 2000 and 2010. The areas shaded in grey represent the standard error of the mean

Table 2 Comparisons of resin duct total area (mm^2 $year^{-1}$) between live and dead sugar pine by time window

	Live	Dead	*p* value
5-year time window			
Average	0.337 (0.042)	0.238 (0.021)	0.028*
Trend	0.019 (0.011)	− 0.025 (0.010)	0.010*
COV	0.694 (0.078)	0.714 (0.069)	0.778
10-year time window			
Average	0.320 (0.037)	0.275 (0.020)	0.268
Trend	0.007 (0.003)	− 0.015 (0.004)	< 0.001*
COV	0.656 (0.060)	0.643 (0.037)	0.839
25-year time window			
Average	0.318 (0.034)	0.291 (0.020)	0.463
Trend	0.001 (0.002)	− 0.002 (0.001)	0.043*
COV	0.686 (0.043)	0.612 (0.025)	0.136
50-year time window			
Average	0.307 (0.028)	0.295 (0.019)	0.644
Trend	0.001 (0.001)	− 0.001 (0.001)	0.217
COV	0.693 (0.044)	0.602 (0.024)	0.061

Values in parenthesis are standard error. Significant differences between live and dead sugar pine are based on paired *t* tests and are highlighted by an asterisk

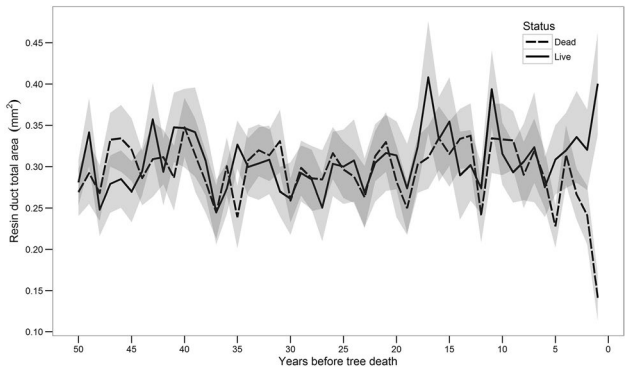

Fig. 4 Average resin duct total area for dead (dashed) and live (solid) sugar pine 50 years before tree death. Years before tree death were based on the year of mortality for the dead tree within each pair of live and dead sugar pine. The trend (i.e. slope) of resin duct total area during the 10 years before tree death was significantly different than in dead sugar pine, where the trend in resin duct total area was negative in dead sugar pine and positive in live sugar pine. The areas shaded in grey represent the standard error of the mean

of resin duct total area was negative in trees that died and positive in trees that lived. The greatest difference in the trend of resin duct total area occurred during the 10-year time window when resin duct total area in sugar pine that died decreased at an annual rate of 0.0154 mm^2 $year^{-1}$, while sugar pine that lived increased in resin duct total area by 0.0068 mm^2 $year^{-1}$ ($p < 0.0001$). Resin duct size was lower in trees that died but the difference was not significant, and the 50-year trend in resin duct size changed very little

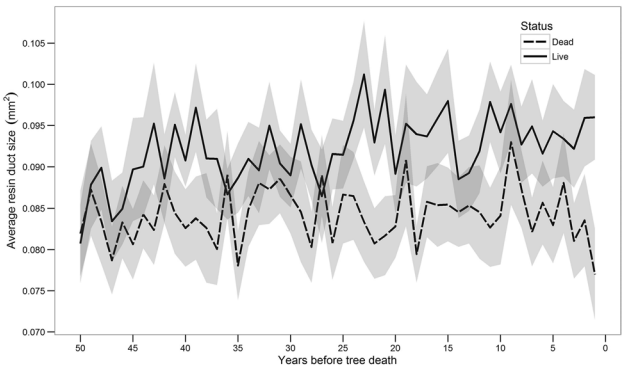

Fig. 5 Average resin duct size for dead (dashed) and live (solid) sugar pine 50 years before tree death. Years before tree death were based on the year of mortality for the dead tree within each pair of live and dead sugar pine. The 10-year trend and 50-year variability in resin duct size were significantly lower in dead sugar pine than live sugar pine

Table 3 Comparisons of resin duct size (mm^2 $year^{-1}$) between live and dead sugar pine by time window

	Live	Dead	*p* value
5-year time window			
Average	0.0829 (0.0053)	0.0713 (0.0041)	0.092
Trend	− 0.0021 (0.0020)	− 0.0058 (0.0022)	0.184
COV	0.4153 (0.0837)	0.4527 (0.0769)	0.654
10-year time window			
Average	0.0831 (0.0047)	0.0768 (0.0042)	0.349
Trend	− 0.0005 (0.0008)	− 0.0024 (0.0008)	0.041*
COV	0.3924 (0.0603)	0.3534 (0.0423)	0.546
25-year time window			
Average	0.0834 (0.0042)	0.0781 (0.0037)	0.355
Trend	< 0.0001 (0.0003)	− 0.0003 (0.0002)	0.068[W]
COV	0.3984 (0.0404)	0.3346 (0.0298)	0.165
50-year time window			
Average	0.0824 (0.0036)	0.0790 (0.0035)	0.495
Trend	< 0.0001 (0.0001)	− 0.0001 (< 0.0001)	0.100[W]
COV	0.3994 (0.0371)	0.3116 (0.0247)	0.033*

Values in parenthesis are standard error. Significant differences between sugar pine that lived and died are highlighted by an asterisk and were based on paired *t* tests or Wilcoxon signed-rank tests

[W]Differences between live and dead sugar pine were tested using Wilcoxon signed-rank test

for both live and dead trees (Fig. 5). However, the 10-year trend of resin duct size was significantly lower in sugar pine that died (− 0.0024 mm^2 $year^{-1}$) compared to sugar pine that lived (− 0.0005 mm^2 $year^{-1}$, $p = 0.0409$, Table 3). Additionally, resin duct size in sugar pine that lived also showed

Table 4 Suite of predictor variables considered in candidate logistic regression mortality models for large sugar pine

Variable	Type	Abbreviation
50-year average of BAI	Growth	BAI_50
10-year trend of BAI	Growth	BAI_slp10
5-year variability of BAI	Growth	BAI_cov5
50-year count of abrupt growth declines	Growth	DEC_50
5-year average of resin duct total area	Defense	TA_5
10-year trend of resin duct total area	Defense	TA_slp10
50-year variability of resin duct total area	Defense	TA_cov50
5-year average of resin duct size	Defense	Size_5
10-year trend of resin duct size	Defense	Size_slp10

All variables had a variance inflation factor value of < 2.0 when analyzed in the full model

BAI basal area increment (see Eq. 1)

greater 50-year coefficient of variation than trees that died ($p = 0.0334$).

Large sugar pine mortality models

Candidate models for sugar pine mortality included nine different growth and defense variables (Table 4). There were four models within two AICc of the top mortality model and four of five top models included growth and defense variables (Table 5). One of the top models only contained growth measures (BAI_slp10, BAI_cov5, DEC_50). However, combinations of growth and defense variables in large sugar pine mortality models were generally more informative than either growth or defense variables alone. Growth and defense averages were not included in any of the top models and the probability of sugar pine mortality was better informed by trends and variability in growth and defense. All of the top models included variables with short-term time windows (5- and 10-year) and the only longer-term time windows (25- and 50-year) included the number of abrupt growth declines and coefficient of variability in resin duct size in the 50-year time window.

The top model included the 10-year trend of basal area increment, the 5-year coefficient of variation of basal area increment, and the 10-year trend of resin duct total area (Table 6). The area under the receiver operator characteristic curve was 0.85 for the top model, and correctly classified 66.7 % of trees that died, 84.8 % of live trees, and 75.8 % of all trees. The relative strength in the top model variables, based on standardized coefficient estimates, were the 10-year trend of resin duct total area (2.35), followed by 10-year trend of basal area increment (2.14), and weakest for the 5-year coefficient of variation of basal area increment (− 1.90).

Table 5 Summary of the top sugar pine mortality models

Model	Model type	*K*	AICc	Δ AICc	AICc wt	LL	ROC	Cut point	Trees correctly classified (%)		
									Dead	Live	Total
DBH + BAI_slp10 + BAI_cov5 + TA_slp10	Growth and defense	5	72.16	0.00	0.20	− 30.56	0.85	0.55	66.6	84.8	75.8
DBH + BAI_slp10 + BAI_cov5 + DEC_50 + TA_slp10	Growth and defense	6	72.56	0.40	0.16	− 29.57	0.84	0.55	66.6	81.8	74.2
DBH + BAI_cov5 + TA_slp10	Growth and defense	4	73.06	0.90	0.13	− 32.20	0.83	0.55	69.7	84.8	77.2
DBH + BAI_slp10 + BAI_cov5 + DEC_50	Growth only	5	73.32	1.16	0.11	− 31.16	0.84	0.40	69.7	72.7	71.2
DBH + BAI_slp10 + BAI_cov5 + TA_slp10 + TA_cov50	Growth and defense	6	74.15	1.99	0.07	− 30.36	0.84	0.48	69.7	75.8	72.7
DBH + TA_slp10 + TA_cov50	Defense only	4	80.91	8.75	< 0.01	− 36.12	0.77	0.45	69.7	69.7	69.7

All models were built using logistic regression and the top model was selected using Akaike's Information Criterion with a correction for small samples sizes (AICc). See Table 4 for a description of predictor variables. K is the number of parameters

Δ*AICc* is the difference from the top model, *AICc wt* is the weight of each model, *LL* is the log likelihood, and *ROC* is the area of the receiver operator characteristic curve

Table 6 Prediction variables for the top logistic regression mortality model for large sugar pine

Predictor	Coefficient estimate	Standard error	*p* value	Standardized coefficient	VIF
Intercept	1.11	1.12	0.32	0	–
DBH	0.01	< 0.01	0.28	0.73	1.19
10-year trend of BAI	0.44	0.30	0.14	2.14	1.24
5-year variability of BAI	− 9.73	4.35	0.02	− 1.90	1.20
10-year trend of resin duct total area	48.86	23.07	0.03	2.35	1.49

The standardized coefficient, in terms of standard deviation, is calculated post hoc, and offers an estimate of the strength of the effect of each variable on the probability of large sugar pine mortality

VIF is the variance inflation factor

Discussion

Differences between live and dead

While a lower short-term average growth rate is commonly associated with tree mortality across a wide range of species (Cailleret et al. 2017), in our study, we found that temporal patterns of growth rather than average growth rates differed most between sugar pine that lived and died. Large sugar pine that died tended to have a declining growth trend, but also higher year-to-year growth variability, and more abrupt declines in growth. The greatest difference was found in the 10-year growth trend, suggesting that large sugar pine that died experienced a declining growth trend that was not present in paired sugar pine that lived. This result is consistent with other research on conifers that found decreasing growth trends to be associated with tree mortality (Bigler and Bugmann 2003; Das et al. 2007; Kane and Kolb 2014; Cailleret et al. 2017). Sugar pine that lived also had lower growth variability in the 5 and 10 years preceding mortality in trees that died, signifying less sensitivity to changes in the environment that affect resource availability. An association between mortality and higher growth variability 5 and 10 years before mortality has been reported in limber pine in northern Arizona (Kane and Kolb 2014). Ogle et al. (2000) also found that pinyon pine with more variability in recent growth were more likely to die. Considering that live and dead tree pairs in our study were of similar size, experienced the same climate, and were growing under similar environmental conditions (e.g., competition), strong fluctuations and negative declines in growth may reflect some type of physiologically driven signature of disruption in tree vigor or inadequate allocation to carbohydrate storage.

One exception to the prevalence of short-term growth to inform mortality in our study was the detection of faster growth more than 10 years prior to mortality in the dead tree of each pair (Fig. 3). This pattern suggests that trees that disproportionately allocated to growth early on may lack sufficient carbohydrate storage necessary to survive when conditions change decades later. The strength and duration of this pattern is quite interesting, warranting further inquiry. Sugar pine that died also tended to have a higher occurrence of abrupt growth declines over 50 years. Pedersen (1998) first demonstrated the association of abrupt declines with tree mortality in oaks and suggested that past events that lead to sudden and substantial decreases in growth may indicate that the tree contains insufficient reserves to withstand subsequent stress that can lead to mortality.

Reduced susceptibility to mortality in trees with stable growth trends, lower growth variability, and fewer abrupt declines may reflect differences in stomatal regulation and carbon allocation patterns. For instance, Scots pine (*Pinus sylvestris*) that maintained relatively high carbon assimilation rates with greater water loss during an experimental drought had a lower probability of mortality than individuals with more conservative assimilation rates (Garcia-Forner et al. 2016). Many studies have also shown that living conifers often maintain stomatal conductance during drought and have increased non-structural carbohydrates than dying conifers (Adams et al. 2017; Galiano et al. 2017; Timofeeva et al. 2017). Thus, trees with more consistent allocation to radial growth under stressful conditions may also more consistently allocate carbon to storage (e.g., large roots and non-structural carbohydrates) and resource acquisition organs (e.g., leaves and fine roots) that can reduce the susceptibility to mortality.

Large sugar pine that died did not sustain allocation to resin duct defenses. This study is the first to demonstrate the importance of resin duct trend and variability related to conifer mortality. While the metrics of defense in our study differed, the importance of defense is consistent with recent studies on other pine species that found relevant differences in average resin duct characteristics related to mortality in pines (Kane and Kolb 2010; Ferrenberg et al. 2014; Hood et al. 2015). More resin duct area is associated with greater resin flow (Hood and Sala 2015), and sugar pine with more resin duct total area may be more successful at pitching out bark beetles by having more resin available (Nebeker et al. 1992; Strom et al. 2002; Perrakis and Agee 2006). We did not find a significant difference in average resin duct size

between sugar pine that lived and died; however, resin duct size in dead sugar pine decreased more rapidly in the 10 years before mortality. Applying Poiseuille's law to resin flow, where decreases in resin duct diameter will decrease resin flow by the fourth power (Schopmeyer et al. 1954), indicates that subtle reductions in resin duct size may have important implications on resin flow. Large sugar pine with a declining trend in resin duct size could be increasingly less successful in resisting bark beetle attack because of higher resistance in flow, even when resin duct production is constant or similar to live trees. Resin duct size in trees that lived also had more year-to-year variability (i.e. greater sensitivity) over a 50 year time period. Considering that annual variation in resin duct size in sugar pine has been negatively associated with climate water deficit (Slack et al. 2017), the ability of a tree to alter the size of resin ducts produced in a given year based on the availability of water resources may be of importance to survival. For example, producing larger resin ducts during wet years and smaller resin ducts during dry years may represent a more effective strategy to reduce mortality risk than consistently producing resin ducts that are equal in size from year to year. The ability to produce larger resin ducts when resources are available could lower mortality risk because larger resin ducts are associated with a greater capacity to synthesize and store resin.

Large sugar pine mortality models

To our knowledge, this is the first study that compared the relative importance of growth and defense allocation in association with sugar pine mortality. Our findings are consistent with Ferrenberg et al. (2014) who also found that growth and defense measures informed mortality models in lodgepole pine and limber pine. While defense measures were included in most of the top mortality models, multiple measures of growth pattern were collectively more informative and a growth only model was equally informative (Table 5). We were somewhat surprised to find that growth explained more variation in mortality because trees resistant to bark beetle attack have been shown to devote more xylem area to resin ducts in other species (Hood et al. 2015), and previous research has found resin duct defenses to better predict mortality than growth (Kane and Kolb 2010). Broader generalizations on the relative importance of growth and defense associated with tree mortality requires additional examination, but likely reflects differences among species, climatic regions, level of bark beetle activity, tree age, and other factors.

While our results indicated that short-term measures of tree growth and defense were more informative, other studies have found both short- and long-term growth to be informative (Bigler and Bugmann 2003; Kane and Kolb 2014), and Das et al. (2007) found long-term growth trends (40 years) to be more informative for sugar pine specifically. Kane and Kolb (2014) also concluded that a mixture of time frames could best predict mortality in mixed-conifer forests of the southwestern United States. However, the importance of short- or long-term growth and defense measures may shift over time and space depending on the size of the bark beetle population (endemic or outbreak population levels), tree age, and genotypic variation. For example, recent evidence in ponderosa pine found that selection by mountain pine beetles before and after an outbreak shifted from slow-growing tree genotypes to fast-growing genotypes (de la Mata et al. 2017). It is also likely that genetic differences in tree vigor and its ability to cope with stress and other factors contributed to survival and mortality in sugar pine. The link between genetics and measures of tree vigor has been documented in conifers for both growth (e.g., Li et al. 2015) and resin duct defenses (e.g., Westbrook et al. 2015).

Understanding the role of vigor measures for tree mortality is of increasing importance considering that many western US pine forests will likely continue to experience stress from numerous factors. Fire exclusion has substantially altered forest structure and increased competition in many areas. At our study site in particular, the historical frequent fire regime has been absent for over 120 years, leading to densification and infilling of primarily white fir and incense cedar (Knapp et al. 2013). Competition was not informative in our models; this was likely because of insufficient variability in competition due to our paired study design. We expect that sugar pine with more competition would result in a higher probability of mortality (Das 2012) and that increasing competition in areas that continue to be fire excluded would likely contribute to further reductions in tree vigor and increased mortality in large sugar pine. Additionally, trends in conifer mortality will continue to be influenced by periods of drought and bark beetle outbreaks. This trend is perhaps most recently exemplified by the extended drought in California from 2012 to 2015 that resulted in extensive forest mortality (Young et al. 2017). Given this scenario, managers will be increasingly tasked with promoting forest conditions that are more resilient to future disturbances. Our results indicate that effective treatments to reduce the probability of mortality in pines will likely need to consider responses of both growth and defense.

While our study was conducted immediately prior to subsequent treatments of thinning and burning, and we, therefore, did not examine the impacts of treatments on mortality, our results may provide some potential insights for managers. Surviving trees had growth and defense characteristics that increased or only slightly declined during the 10 years preceding mortality. Treatments, such as thinning and burning, that can promote these growth and defense characteristics in large sugar pine may be an effective solution to limit mortality, at least during endemic or background bark

beetle levels. For instance, resin duct defenses have been shown to be higher following repeated low intensity wildfire compared to unburned areas (Hood et al. 2015) and in areas that had a combination of forest thinning and prescribed fire treatments (Hood et al. 2016). Our findings that mortality was largely informed by recent patterns of allocation to growth and defense suggests treatments may effectively reduce the probability of mortality if trees respond quickly by limiting declines in growth and defense over time, but the mechanistic underpinnings still need further examination.

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Author contribution All authors contributed to the study concept and design. Data collection and analysis were performed primarily by AWS with some assistance from JMK. The first draft of the manuscript was written by AWS and all authors helped improve the manuscript in subsequent versions. All authors read and approved the final manuscript.

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