

LARGE SUGAR PINE (*PINUS LAMBERTIANA*) VIGOR AND MORTALITY IN A
FIRE-EXCLUDED FOREST OF THE CENTRAL SIERRA NEVADA

By

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A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Forestry, Watershed & Wildland Sciences

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May 2016

ABSTRACT

LARGE SUGAR PINE (*PINUS LAMBERTIANA*) VIGOR AND MORTALITY IN A FIRE-EXCLUDED FOREST OF THE CENTRAL SIERRA NEVADA

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In recent decades rapid environmental change has led to significant shifts in forest dynamics across the western United States. In particular, fire exclusion has led to denser forests with higher competitive stress, and climate change has increased temperatures, and affected water availability by altering snowmelt and evapotranspiration. As a result tree vigor for many species has declined and contributed to increased rates of tree mortality, especially for large and old trees. Large trees provide important ecological services, but are rare on the landscape due to past logging activities. Therefore, forest managers have focused restoration efforts to improve old-growth forests conditions. However, the impact of environmental stress on tree vigor and mortality is a complicated process and more information about the relative importance of climate and competition is needed.

This study investigated tree vigor and mortality for large sugar pine (*Pinus lambertiana*) in response to climate and competition at the Stanislaus-Tuolumne Experimental Forest in the Sierra Nevada. This mixed-conifer forest has experienced a long period of fire exclusion and increased warming that has likely contributed to greater vulnerability of large sugar pine to pathogen (e.g. white pine blister rust) and bark beetle attacks. Tree vigor was examined by analyzing annual measurements of

growth (i.e. basal area increment, BAI) and resin duct defenses. Chapter 1 examined the response of large sugar pine growth and defense to climate (i.e. temperature, precipitation, climatic water deficit), and retrospective competition using generalized linear mixed models. Chapter 2 modeled the relative importance of growth, defense, and competition on the probability of large sugar pine mortality using logistic regression.

Reduced BAI in large sugar pine was more strongly associated with lower January temperatures, less precipitation from the previous October through December, higher interspecific competition, and higher intraspecific competition ($R^2 = 0.81$, RMSE = 9.96). Resin duct size was most associated with water deficit, precipitation from the previous October- current April, and total competition ($R^2 = 0.66$, RMSE = 0.022). Resin duct total area was associated with water deficit, precipitation from the previous October- current April, total competition, and the interaction of total competition with June temperature ($R^2 = 0.54$, RMSE = 0.2108). Measures of competition had a stronger relationship with large sugar pine growth and defense when compared to measures of climate. The best model of large sugar pine mortality included growth, defense, and competition variables. Declining growth (i.e. the slope of BAI) and lower growth variability during the 10 years before mortality had the greatest association with mortality (area under ROC = 0.93). Internal validation of the top mortality model correctly classified 87.9% of dead sugar pine and 84.8% of live sugar pine. Results from this study highlight some of the trade-offs between growth and defense in response to climate and competition, and the importance of declining growth and defense leading to a higher probability of mortality.

ACKNOWLEDGEMENTS

This project was funded and supported by the USDA Forest Service Pacific Southwest Research Station (PSW). First I would like to thank my primary adviser Dr. Jeffrey Kane, who spent countless hours guiding me through many difficult aspects of this project. Dr. Eric Knapp provided support throughout the project, particularly in the field and during the final stages of writing my thesis. Dr. Rosemary Sherriff also provided valuable support and guidance throughout my time at Humboldt State University (HSU). The field work for this project was carried out in the summer of 2014 with help from Nickolas Zeibig-Kichas, and the PSW research field crew, which included Julia Fields, Mark Hilgers, Marissa Vossmer, and Martha Langill. Bob Carlton provided me with essential tools in the field that allowed me to collect large amounts of data in one summer. In the HSU Wildland Fire Lab, Amber Shearer assisted with data processing. Finally, I would like to thank my cohort of graduate students, friends, and family that were a constant source of support during the struggles and accomplishments of this project.

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PREFACE

This thesis is presented in the journal format, and includes two chapters that will be submitted for publication in scientific journals. Therefore, some redundancy exists between chapters, particularly in the references and methods sections. The work for this master's thesis was done independently, and the collective term "we" is used in both chapters instead of "I" because the publication of these chapters will include additional authors. Chapter 1 is titled "Contrasting impacts of climate and competition on large sugar pine growth and defense in a fire-excluded, mixed-conifer forest of the central Sierra Nevada" and is formatted for publication in the journal *Ecosphere*. Chapter 2 is titled "Large sugar pine mortality models informed by growth, defense, and competition in a fire-excluded forest of the central Sierra Nevada", and is formatted for the journal *Forest Ecology and Management*.

INTRODUCTION

The management of old-growth forests in the western United States faces numerous challenges. Factors such as climate change and increased competition related to fire exclusion have increased stress on many forest ecosystems, reducing tree vigor and increasing tree mortality in many regions. However, there are many uncertainties regarding the relative importance of climate- and competition-induced effects on tree growth and resin duct defenses (i.e. tree vigor) that are contributing to forest decline. Even large diameter trees are vulnerable because of greater water demands in environments that are becoming more water limited with increased susceptibility to bark beetle attack. Large and old trees are highly valued for critical wildlife habitat, long-term carbon sequestration, forest diversity, and spiritual and cultural connection, and managers are interested in preserving remaining old-growth forests. Widespread mortality of large diameter trees could have considerable negative ecological and societal consequences, therefore, research on the factors involved in tree stress and mortality is essential to inform policy and management decisions.

This study focused on sugar pine in the central Sierra Nevada, California. Old-growth forests in the Sierra Nevada have declined in recent years and sugar pine, in particular, are underrepresented on the landscape. The factors that influence sugar pine vigor and mortality are poorly understood, and often many predisposing, contributing and inciting factors are involved. Using a retrospective approach for estimating past competition, annual measures of growth and defense are modeled. Large sugar pine

mortality is modeled to analyze various time windows to determine the relative importance of long-term, short-term, recent and past trends in growth, defense, and competition. The results from this thesis provides information on the relative importance of climate and competition of large sugar pine growth and defense. Additionally, analysis of large sugar pine mortality models improves our understanding of the relationships of growth, defense, and competition with sugar pine mortality.

CHAPTER 1: CONTRASTING IMPACTS OF CLIMATE AND COMPETITION ON
LARGE SUGAR PINE GROWTH AND DEFENSE IN A FIRE-EXCLUDED,
MIXED-CONIFER FOREST OF THE CENTRAL SIERRA NEVADA

Abstract

Many forest ecosystems in the western United States have experienced rapid environmental change associated with fire exclusion and increased warming. In particular, large trees that provide important ecological services have declined in certain areas from widespread mortality events. Mortality is often related to reduced tree vigor, which can be caused by factors such as climate and competition for water, light, and other resources. Tree growth and resin duct defenses are closely linked to overall tree vigor and can be used to assess tree response to climate and competition over time. Growth, resin duct defense, and competition data was collected from 113 large diameter (> 50 cm) sugar pine at the Stanislaus Tuolumne Experimental Forest in the central Sierra Nevada of California. This study examined trends in large sugar pine growth and defense from 1964-2012 and monthly and seasonal climate relationships with growth and defense. Generalized linear mixed models were used to determine the relationships of climate and competition with growth (basal area increment) and defense (resin duct size and total area). Additionally, standardized coefficients from the top models were used to determine the relative importance of climate and competition. Large sugar pine growth increased by $0.17 \text{ cm}^2 \text{ y}^{-1}$ ($p = 0.0076$, $R^2 = 0.14$), and resin duct size decreased

by $0.0001 \text{ mm}^2 \text{ y}^{-1}$ ($p = 0.0022$, $R^2 = 0.17$). Growth was most associated with January temperature ($\beta = 0.0041$) and intraspecific competition ($\beta = -0.0064$), while resin duct size and total area were most associated with climatic water deficit ($\beta = -0.4085$, -0.0734) and total competition ($\beta = -0.9571$, 0.8267). Climate change and fire exclusion pose unique management concerns by altering limiting resources. Based on the results of this study, growth will likely continue to increase in response to continued warming. However, resin duct size and total area are likely to decrease in response to climate change. Higher competition could trigger sugar pine to allocate more to resin duct total area, but limit the size of individual resin ducts. Thinning treatments that reduce intraspecific competition could increase growth. However, reducing total competition could result in larger resin ducts that cover less total area, possibly leading to a greater efficiency in resin flow, but a smaller reservoir of resin.

Introduction

In recent decades many forest ecosystems in the western United States have experienced environmental changes that can often increase tree stress, and lead to elevated tree mortality. In particular, forest declines have been linked to climatic water deficit and drought events associated with changes in temperature and precipitation (van Mantgem et al. 2009; Allen et al. 2010; Smith et al. 2015). Additionally, a century of fire exclusion has altered the structure and composition of many forested landscapes, leading to denser forests with higher competition for limited resources. Even large diameter trees that typically have a competitive advantage over smaller trees can become more vulnerable to mortality due to factors attributed to climate change and fire exclusion (Lutz et al. 2009; Lindenmayer et al. 2012; Bennet et al. 2015). In many forest ecosystems the effects of climate change and fire exclusion may exacerbate other disturbances. For example warmer and drier climate conditions coupled with denser forests have increased the occurrence of bark beetle outbreaks (Raffa et al. 2008) and large wildfire events (Westerling et al. 2006).

Due to past logging activities, large diameter trees are rare across most landscapes and are often limited to protected areas, such as national parks (Kolb et al. 2007; Lindenmayer et al. 2012). However, large and old trees provide many valuable ecological and ecosystem services, such as long-term carbon sequestration (Luyssaert et al. 2008) and critical wildlife habitat for many threatened or endangered species (Bart and Forsman 1992; Engstrom and Sanders 1997). From a management perspective larger

trees can increase the capacity of a stand to resist disturbances (Hurteau and North 2008), aid recovery following a disturbance by providing a seed source (Keeton and Franklin 2005), and regulate localized environments (Rambo and North 2009).

Many ecosystems with large, thick-barked pine species typically have a frequent and low intensity fire regime that historically maintained more open stands (Agee 1993). With less competition, limited resources such as water are more available and easier to access, which may have increased the ability of individual trees to survive during prolonged drought and recover following a disturbance (Thomas and Waring 2014). However, the current conditions in many pine dominated forests may have contributed to reduced vigor (e.g. growth and defense) in large diameter trees. Furthermore, many predisposing and contributing factors can influence tree vigor and susceptibility to future disturbances over time (Waring 1987; Manion 1991), complicating assessments of tree vigor. Improving our understanding of the relationship between large tree vigor and environmental stress resulting from climate, competition, and these interactions are crucial for adaptive management under future climate and land use scenarios.

Climate projections indicate rising temperatures in most regions of the western United States (Melillo et al. 2014), driving expected changes in the timing of the growing season and snowmelt, as well as drought intensity and disturbance regimes. These environmental changes could alter available resources and impact pine tree response and vigor. Thinning and prescribed fire treatments have been implemented to reduce competition following a period of fire exclusion to increase stand resiliency to future disturbance (Agee and Skinner 2005). Information on the relationship of climate

and competition with large pine vigor in fire-excluded forests will be valuable to forest managers interested in evaluating the effectiveness of treatments across a landscape and developing management plans in an uncertain future.

Dendrochronology methods that measure annual growth patterns in individual trees provide an opportunity to examine multiple characteristics of vigor over time. Tree growth has been linked to mortality for many tree species, where a higher probability of death is associated with declining growth trends (Bigler and Bugmann 2004; Hanna and Kulakowski 2012; Kane and Kolb 2014), slower relative growth (Pederson 1998; Bigler and Bugmann 2003), and more abrupt declines (Das et al. 2007). Furthermore, the same methods can be used to measure annual variation in resin duct defenses. Resin ducts are important in defending many conifer species against insect and pathogen attack by producing oleoresins that chemically impair, isolate, and expel invading pests (Francechi et al. 2005). Previous research has shown a strong link between increased tree allocation to resin ducts (i.e. larger or more resin ducts) and decreased probability of mortality for many pine species (Kane and Kolb 2010; Gaylord et al. 2013; Ferrenberg et al. 2014, Hood et al. 2015). However, more information is still needed on how resin ducts respond to environmental changes, such as climate and competition.

There is a high carbon cost associated with producing resin and resin ducts that may lead to trade-offs between allocating carbon to tree growth and defense (Strauss et al. 2002). When considering the resource availability hypothesis, constitutive (i.e. always present) defenses may be more common in slower growing trees when the cost of replacing tissues is high, while inducible defenses (i.e. produced in reaction to stress)

may occur in faster growing trees (Endara and Coley 2011). Another theoretical framework, the growth-differentiation balance hypothesis (GDBH) suggests that when resources become limited due to stress (e.g. higher competition), reducing growth but not photosynthesis, more carbohydrates will be available for defense (Herms and Mattson, 1992). Resin ducts in many pine species have been shown to follow similar patterns (Gaylord et al. 2013, Hood et al. 2015), and these hypotheses can help explain the complicated trade-offs between growth and defense.

The relationship between tree growth and climate has been widely studied for many pine species, but seasonal or monthly climate-growth relationships are highly variable. Growth variability for many pine species in northern California is most associated with winter precipitation and summer temperature (Yeh and Wensel 2000). Whereas longleaf pine growth in the southeastern U.S. is most limited by low values for drought indices and lower precipitation during summer and early fall (Henderson and Grissino-Mayer 2008). Furthermore, in the last half of the twentieth century conifer growth at high elevations in California has been shown to be more variable than any time in the past 1000 years, and positively correlated with increasing temperatures (Bunn et al. 2005). This study provides evidence that climate-growth relationships are responding to climate change. Competition has been shown to limit growth for many species (Contreras et al. 2011, Sanchez-Salguero et al. 2015, Zhang et al. 2015), but competition-growth relationships can vary among species (Das 2012).

The relationship between climate and resin duct defenses has been studied for Norway spruce where resin duct density was higher following a wet spring and a warm

summer (Wimmer and Grabner 1997). In the United States, resin duct total area was higher during warmer and wetter conditions in July for ponderosa pine in Montana (Hood et al. 2015), and following a wetter November of the previous year for longleaf pine in Florida (Slack et al. 2016). To our knowledge, there is no research examining the relationship between competition and resin duct defenses.

This study focused on large diameter sugar pine (*Pinus lambertiana*) in the central Sierra Nevada where the effects of climate change and fire exclusion are evident. Increasing temperatures associated with climate change in the Sierra Nevada have the potential to alter hydrological patterns (Stewart et al. 2004) and increase climatic water deficit (Lutz et al. 2010), limiting water availability. Furthermore, a century of fire exclusion in the Sierra Nevada has allowed shade tolerant and less fire tolerant species such as white fir (*Abies concolor*) to establish in the understory of mixed-conifer forests, resulting in denser stands with greater competition (Smith et al. 2005; Knapp et al. 2013; McIntyre et al. 2015). These conditions alone and in combination with other factors (e.g. white pine blister rust, *Cronartium ribicola*), are having a negative impact on sugar pine populations (van Mantgem et al. 2004).

Growth has been widely studied for sugar pine, and in particular the growth response to competition (Das et al. 2012) and as a measure of pre-fire vigor (Nesmith et al. 2015). However, few studies have collectively compared the influence of competition and climate on tree growth (Gómez-Aparicio et al. 2011; Sanchez-Salguero et al. 2015; Zhang et al. 2015), and to our knowledge no studies have examined the relative importance of climate and competition of resin duct defenses. This study took a

retrospective approach to reconstruct past estimates of competition to analyze the influence of climate and competition at an annual resolution. The primary objective of this study was to examine trends of growth and defense in large sugar pine and to determine the relative importance of climate and competition on these measures of vigor. Specifically, this study focused on the following questions:

- 1) What are the trends in large sugar pine growth and defense over the past 50 years?
- 2) What is the relationship between seasonal and monthly variables of climate and measures of large sugar pine growth and defense?
- 3) What variables of climate and competition are most associated with changes in large sugar pine growth and defense?

Methods

Study area

This study was conducted within the Stanislaus-Tuolumne Experimental Forest (STEF; 38°10'22"N, 120°00'00" W; Figure 1.1) on the western slope of the Sierra Nevada near Pinecrest, California. The experimental forest encompassed 640 ha of mid-elevation (1585 to 1890 m), mixed-conifer forest, and representative of forest types commonly found in the region. The Mediterranean climate consists of warm, dry summers and cold, wet winters. During the time period examined by our study, air temperatures ranged from -8.8 to 28.8°C with an annual average of 8.6°C, and annual precipitation ranged from 364 mm to 2202 mm (annual average of 1146 mm; PRISM, created 28, October, 2015), which mostly fell as snow during the winter months. During exceptional winters, large snowpacks, up to 3 m deep, can result in a shortened growing season from mid-May to the end of September. Soils were loam to gravelly loam of the Wintoner-Inville families complex, and formed primarily from granite, creating a deep, well-drained, and highly productive site (Knapp et al. 2013). The most abundant overstory tree species were *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr. (white fir), *Calocedrus decurrens* (Torr.) Florin (incense cedar), *Pinus lambertiana* Douglas (sugar pine), *Pinus ponderosa* Laws (ponderosa pine), *Pinus jeffreyi* Balf. (Jeffrey pine), and *Quercus kelloggii* Newb. (California black oak). In the fall 2012, a thinning treatment was applied to approximately 80% of the study site. The treatment retained larger diameter trees and removed mostly small diameter white fir and incense cedar that

had established in the absence of fire. The historical fire regime of STEF had a median return interval between 5 and 8 years, but the stand has not experienced a fire since 1889 (Knapp et al. 2013).

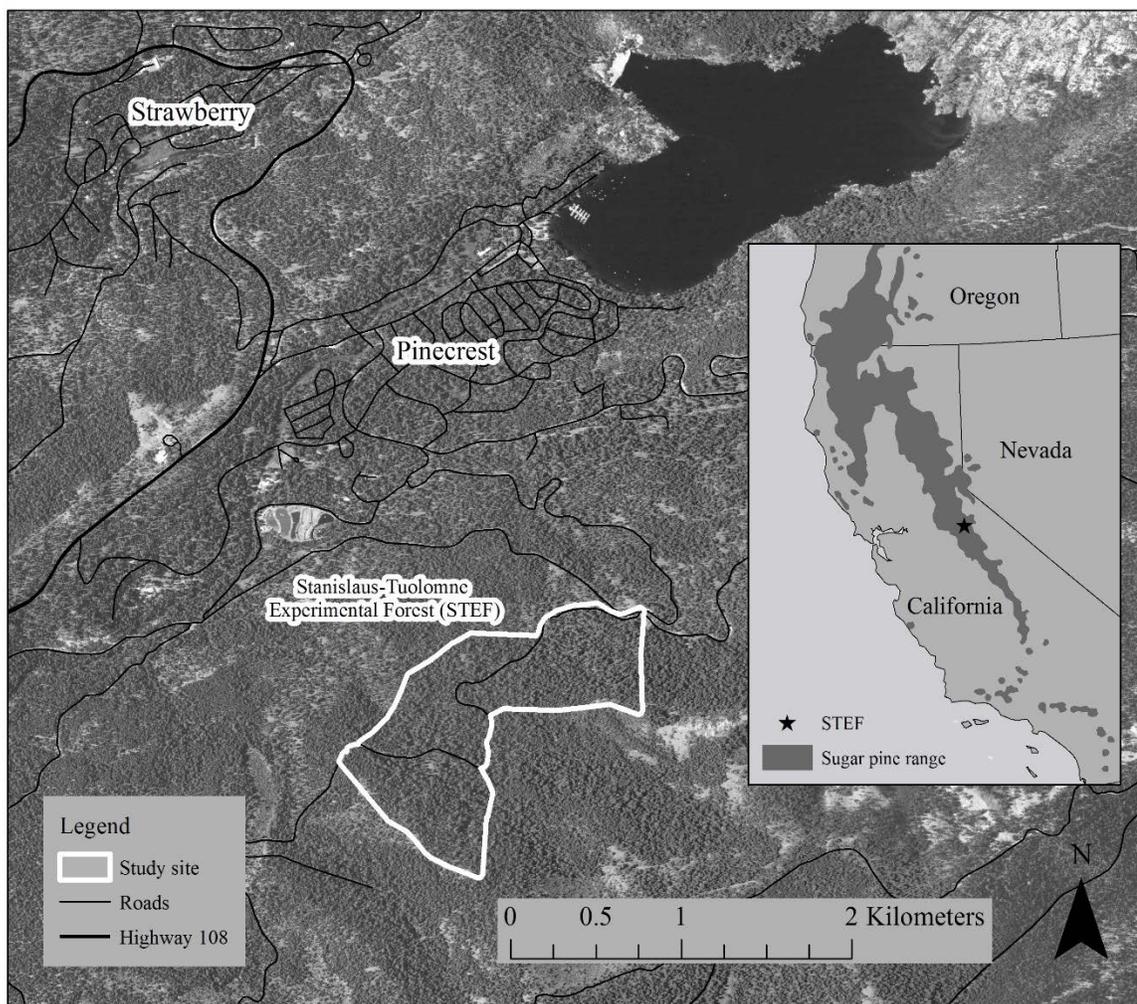


Figure 1.1. Map of the Stanislaus-Tuolumne Experimental Forest (STEF) located near Pinecrest, California. The study site is encompassed by the white polygon.

Data collection

Eighty mature sugar pines with a diameter at breast height (DBH; approx. 1.37 m above the ground) greater than 50 cm were randomly selected within a section of the experimental forest that covered approximately 55 ha. An additional thirty-three large sugar pine were included from a mortality study that selected trees by pairing live sugar pine with all dead sugar pine that met the sampling criteria (see Chapter 2). The final data set for this study included a total of 113 trees. For all sampled sugar pine, we recorded DBH (cm), bark thickness (cm), and extracted one large diameter (12 mm) core to measure annual growth and resin duct defense for each tree. To measure the competition surrounding each sugar pine, a nested fixed area plot was established with the subject tree as the plot center to account for larger trees having a broader influence. We included all competitor trees taller than breast height within 5 m of plot center, all trees with a DBH greater than 5 cm within 10 m, and large diameter trees with a DBH greater than 50 cm within 20 m (Figure 1.2). For each competitor tree, we recorded species, DBH, basal diameter, status (live, dead, cut in 2012), distance and azimuth to subject tree. For all standing dead trees we recorded decay class, which was modified from a previous study (Imbeau and Desrochers 2002) to only include categories for dead trees (snags). A total of 586 uncut competitor trees (10.1% of all measured competitor trees) were cored to the pith (tree center) at breast height using a small diameter (5 mm) increment borer for the purpose of retrospectively estimating competition. The cored competition trees represented the species composition of the whole study area, and

included 222 white fir (19 dead), 137 incense cedar (20 dead), 147 sugar pine (13 dead), 41 Jeffrey pine, 38 ponderosa pine, 1 California black oak, and 1 mountain maple.

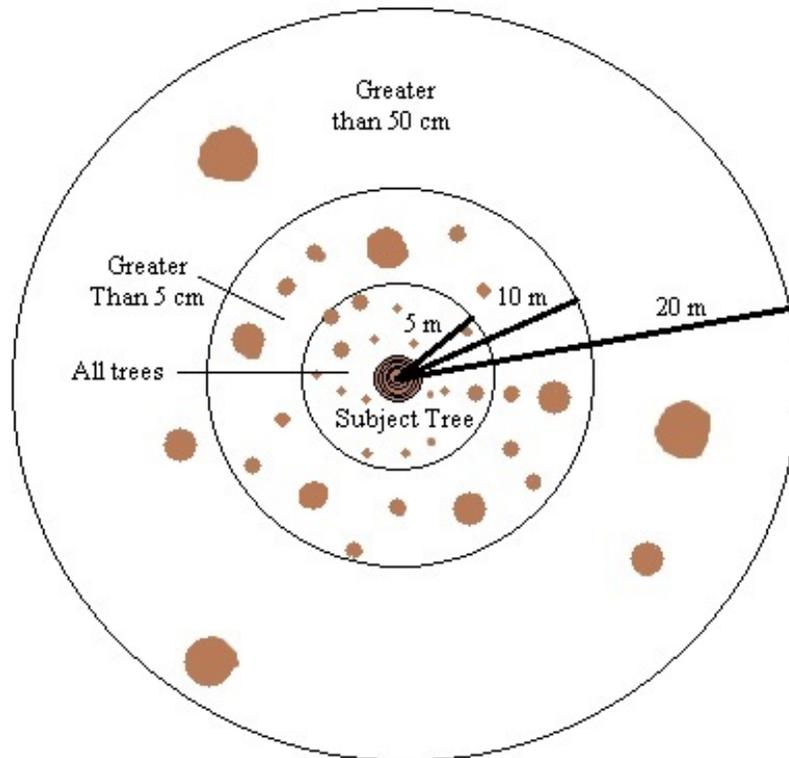


Figure 1.2. Layout of nested fixed area competition plots describing the factors for including a tree based on diameter at breast height.

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 (1,200 dpi) image. Each image was analyzed in the program WinDendro (Regent Instruments 2014), where annual ring boundaries were assigned and total ring width (mm y^{-1}) was measured. All cores were

visually crossdated and COFECHA (Grissino-Mayer 2001) was used to assess potential errors in assigning years to annual rings. The series for all live subject sugar pines (n = 113) had an intercorrelation of 0.552 and a mean sensitivity of 0.177.

Sugar pine growth was calculated as basal area increment (BAI, $\text{cm}^2 \text{y}^{-1}$):

$$\text{Equation 1: } \quad BAI_t = \pi(R^2 - r^2)$$

Where BAI_t was growth for year t, R was the outer radius, and r was the inner radius.

This equation assumed that annual rings had constant ring width and were geometrically circular. BAI was used as a standardization method to account for age- or size-related growth trends while still maintaining suppression or release events that may be related to changes in climate or competition (Biondi and Qeadan 2008, Speer 2010). Sugar pine defense was estimated through measurements of vertical resin ducts within each annual tree ring. Resin ducts were identified and measured from high resolution images of each core using the program ImageJ (Rasband 2014). Annual measurements included the count of identified resin ducts (production, # ducts y^{-1}), the mean size of all resin ducts (size, $\text{mm}^2 \text{y}^{-1}$), and the sum of resin duct area (total area, $\text{mm}^2 \text{y}^{-1}$).

Climate and competition

Climate data were acquired from the Parameter- Elevation Regression on Independent Slopes Model (PRISM, created 28, October, 2015). PRISM used the network of instrumental observations and digital elevation models (DEM) to produce datasets for values of precipitation and temperature at various spatial resolutions. Monthly total precipitation (mm) and monthly temperature (mean, maximum, and

minimum; C°) were extracted from PRISM for the specific study site location (38°10'22"N, 120°00'00" W). Furthermore, to include a measure of relative dryness we estimated the annual climatic water deficit using the water balance model that was first presented by Dyer (2009). Climatic water deficit is defined as the difference between potential evapotranspiration and actual evapotranspiration (PET - AET), and considers seasonal variability in temperature and precipitation, timing in snowmelt, and soil water holding capacity. Climatic water deficit estimates water availability and has been shown to be a biologically important measure of water stress in the Sierra Nevada (Stephenson 1998; Lutz et al. 2010; Das et al. 2013).

To examine the influence of competition related to fire suppression, we retrospectively reconstructed competition by estimating the diameter inside bark (DIB, measured at breast height) for every individual competitor tree going back to 1964 (50 years before the sampling). First, to account for the thinning treatment that occurred in 2012, we measured the basal diameter for all live trees and built site-specific regression models for each species to estimate the DBH for all cut competition trees (Appendix A). Site and species-specific bark equations were then constructed (Appendix A) to estimate bark thickness for all competitor trees that were not cored and to estimate the diameter inside bark for the last year of growth. The last year of growth was estimated for each standing dead competitor by constructing species-specific equations based on the relationship between the last year of growth in cored samples and associated decay class (Appendix A). We could not extract viable cores from dead trees that had fallen, which may have contributed to underestimates of competition during the time period analyzed.

Once the diameter inside bark during the last year of growth was estimated for all competitor trees, mean ring widths were then progressively subtracted to estimate DIB for each year. Mean ring width for each year was estimated by species and tree size using the 586 collected competition cores. Analysis of variance (ANOVA) results showed that mean ring width was not statistically different among three or five different size classes for incense cedar, sugar pine, Jeffrey pine, and ponderosa pine, but was different between the three size classes for white fir (Appendix A) .

Competition was calculated using two methods, the distance-dependent Hegyi index, which has been correlated to tree growth in other studies (Biging and Dobertin 1992, Das et al. 2012), and the sum of the basal area of all competitor trees. Preliminary analysis showed that competition estimated by the Hegyi index had a better relationship with large sugar pine growth and defense, and the basal area of competition was dropped from the analysis. The equation for the Hegyi index is:

Equation 2:
$$C_t = \sum_{j=1}^n \frac{DIB_{jt}}{DIB_{it} \times (D_{ij} + 1)}$$

Where C_t is competition during year t , DIB_{it} was the subject tree diameter in year t , DIB_{jt} was the competitor tree diameter in year t , D_{ij} was the distance from the subject tree i to the competitor tree j , and n was the number of competitors. Estimations for competition were also subdivided to estimate interspecific competition (i.e. non-sugar pine competitors), intraspecific competition (i.e. sugar pine competitors), white fir competition, and total competition.

Statistical analyses

The final dataset included annual measurements for growth, defense, climate, and competition starting in 1964 (50 years before sampling) and ending in 2012 to exclude the possible influence of the thinning treatment on growth and defense in subject trees. We chose to analyze this time frame to capture enough climate variability, while limiting the underestimation of competition due to earlier mortality of competition trees. All statistical analyses were performed in the program R (R Development Core Team 2016).

We examined the trends in mean annual growth and defense for all 113 subject trees by year, and calculated the slope using linear regression. To identify which monthly and seasonal variables of temperature and precipitation were best associated with sugar pine growth and defense we used the statistical package *Treeclim* (Zhang and Biondi 2015). The package calculated bootstrapped estimates of the Pearson's correlation coefficient (r) to detect high resolution climatic signals in trees rings.

We determined the response of large sugar pine growth and defense to changes in climate and competition using generalized linear mixed modeling with the *lme4* package (Bates et al. 2014). This statistical approach was appropriate given the non-normal nature of the sugar pine growth and defense data and the nested structure of annual measurements within each subject tree. Basal area increment was the response variable for all growth models, and the response variable for defense models included resin duct size and total area. We decided not to model resin duct production because

production was highly correlated with resin duct total area ($r = 0.83$). All growth and defense models included a log link function in the gamma distribution family. Gamma regression has been successfully used in previous tree growth modeling studies in temperate forests (Gea-Izquierdo and Canellas 2009; Contreras et al. 2011), and longleaf pine resin duct defense models (Slack et al. 2016). Predictor variables for all models included measures of competition and specific climate parameters for growth or defense. The previous year's growth (previous BAI) was included as a covariate in growth models to account for temporal autocorrelation, and current BAI was included in defense models because resin duct measures were not completely independent of growth. Tree was included as a random effect and included a random intercept for each sampled sugar pine. The first models included predictor variables of climate only and competition only to determine how growth and defense were associated with each variable category separately. We then tested models that combined variables of climate and competition, and included interaction terms between predictor variables. In all, we analyzed 30 models for basal area increment, 48 models for resin duct size, and 46 models for resin duct total area. For each response variable we reported the null model, the top four models combining predictors of climate and competition and the top two models for climate only and competition only.

Akaike's information criterion (AIC) was used for model selection, and substantial differences in model fit were indicated by a change in AIC values greater than 2 (Burnham and Anderson 1998). To avoid issues of multicollinearity, highly correlated predictor variables were not included in the same model and were verified

based on a variance inflation factor (VIF) less than 10 (Burnham and Anderson 1998).

Within the top model we provided an estimate of model accuracy and precision by calculating the root mean squared error (RMSE) and the coefficient of determination (R^2) for the relationship between predicted values and actual values of growth and defense. To determine the relative importance of climate and competition, we calculated the standardized coefficients for each variable based on the fitted GLMM using the following equation:

$$\text{Equation 3: } \beta_{s1} = \beta_1 \times \frac{s_1}{s_y}$$

Where 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

Temporal trends and climate relationships

During the time period analyzed (1964-2012), there were significant trends in large sugar pine growth and defense (Figure 1.3). Average BAI significantly increased over time by $0.17 \text{ cm}^2 \text{ y}^{-1}$ ($p = 0.0076$, $R^2 = 0.14$), with the highest average BAI occurring in 2012 (61.99 cm^2) and the lowest average BAI occurring in 1977 (23.71 cm^2). BAI ranged from 0.76 to $176.90 \text{ cm}^2 \text{ y}^{-1}$ with a median of $37.59 \text{ cm}^2 \text{ y}^{-1}$. Resin duct size had a significant negative trend where average resin duct size decreased by $0.0001 \text{ mm}^2 \text{ y}^{-1}$ ($p = 0.0022$, $R^2 = 0.17$). Variability in resin duct size ranged from $0.0152 \text{ mm}^2 \text{ y}^{-1}$ to $0.4010 \text{ mm}^2 \text{ y}^{-1}$ with a median of $0.0950 \text{ mm}^2 \text{ y}^{-1}$. Resin duct total area did not show a significant trend and annual changes remained relatively flat throughout the time period analyzed.

Large sugar pine growth and defense were related to measures of average monthly temperature and total seasonal precipitation (Table 1). BAI had the strongest relationship with temperature during January of the current year ($r = 0.507$), with greater annual growth following a warmer January. Resin duct defenses were most related to total precipitation during the previous October – current April, where resin duct size was larger ($r = 0.506$) and covered more total area ($r = 0.402$) following higher seasonal precipitation.

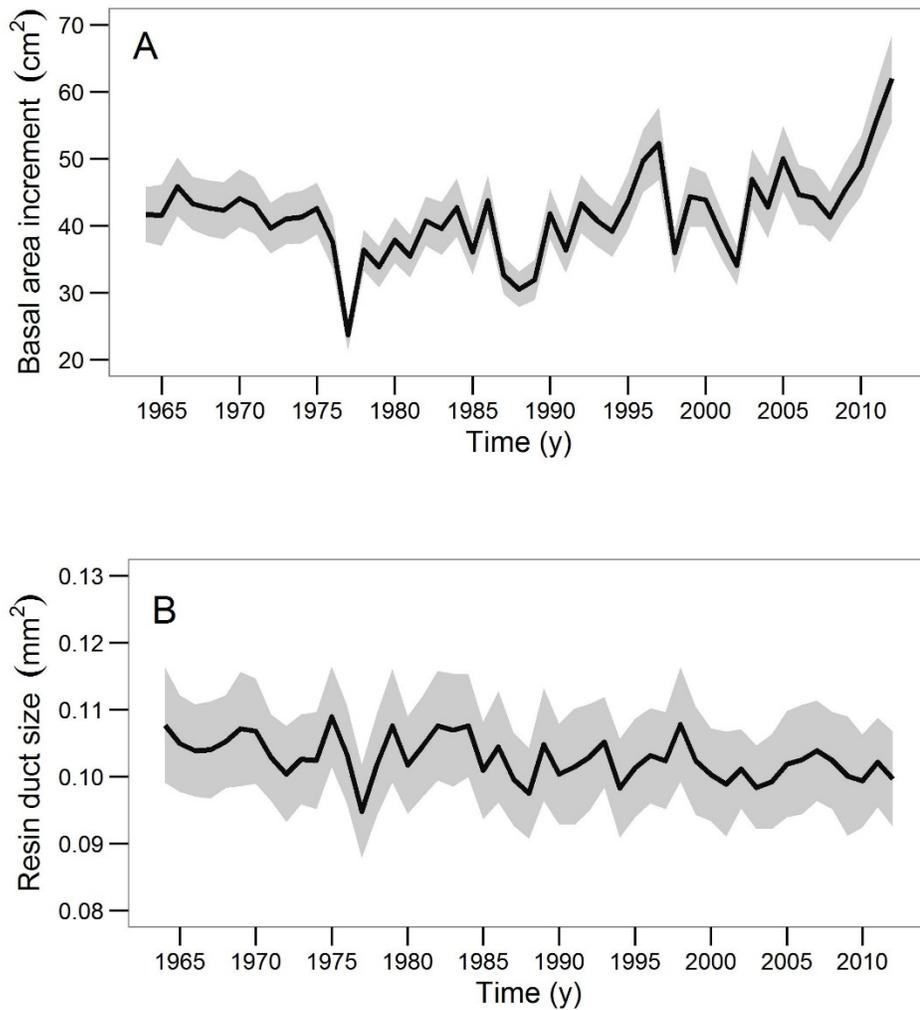


Figure 1.3. Average basal area increment (BAI; A), and average resin duct size (B) from 1964 to 2012. BAI increased by $0.17 \text{ cm}^2 \text{ y}^{-1}$ ($p = 0.0076$, $R^2 = 0.14$) and resin duct size decreased by $0.0001 \text{ mm}^2 \text{ y}^{-1}$ ($p = 0.0022$, $R^2 = 0.17$) during the study's time period. The shaded area represents the 95% confidence interval.

Table 1.1. Significant correlations between climatic factors (temperature and precipitation) and sugar pine growth and defense characteristics.

Variable	Month/Season	Pearson's Correlation Coefficient (r)	Confidence Interval	
			Lower	Upper
Basal Area Increment				
Temperature	Current January	0.507	0.222	0.663
Precipitation	Previous October – December	0.317	0.029	0.529
Resin Duct Average Size				
Temperature	Current April	-0.453	-0.690	-0.135
Precipitation	Previous October – current April	0.506	0.254	0.677
Resin Duct Total Area				
Temperature	Current June	-0.297	-0.535	-0.039
Precipitation	Previous October – current April	0.402	0.135	0.597

Growth and defense models

Analysis of the generalized linear mixed models suggested that the best models for BAI included measures of climate and competition, and consistently had a lower AIC than models based on climate only and competition only (Table 1.2). BAI was more closely associated with models that included the interaction between precipitation and temperature over models that only added precipitation and temperature. Models were improved when total competition was subdivided into interspecific and intraspecific competition. Climatic water deficit had a weak relationship with growth and was not included in any of the top models.

The top model for BAI included January temperature of the current year, total precipitation from the previous fall (October-December), the interaction of January temperature and previous fall precipitation, interspecific competition, and intraspecific competition (Table 1.3, Figure 1.4). The coefficient of determination (R^2) of the relationship between predicted and actual values of BAI was 0.81, and the root mean square error was 9.96 (Table 1.3). Standardized coefficient estimates for the top model indicated that intraspecific competition had the strongest association with BAI ($\beta = -0.0064$), followed by January temperature ($\beta = 0.0041$). The interaction of increasing temperature and precipitation had a dampening effect. For example, January temperature had less of an effect on BAI when precipitation from the previous fall was higher (Figure 1.4 A & B).

Table 1.2. Generalized linear mixed models for basal area increment (sugar pine growth). Predictor variables included January temperature of the current year (Jan temp), total precipitation from the previous fall (Fall precip), the interaction of temperature and precipitation (Jan temp * Fall precip), interspecific competition (Inter comp), intraspecific competition (Intra comp), and total competition (Total comp). All models included the null model of previous basal area increment (Previous BAI) as covariate and Tree as a random effect.

Growth models	K	AIC	Δ AIC	AIC Wt	Log Likelihood
Jan temp + Fall precip + Jan temp * Late precip + Inter comp + Intra comp	9	39605.04	0.00	0.99	-19793.52
Jan temp + Fall precip + Jan temp * Late precip + Total comp	8	39618.76	13.72	0.01	-19801.38
Jan temp + Fall precip + Inter comp + Intra comp	8	39635.35	30.30	0.00	-19809.67
Jan temp + Fall precip + Total comp	7	39647.09	42.04	0.00	-19816.54
Jan temp * Late precip (climate only)	7	39675.11	70.07	0.00	-19830.56
Jan temp + Late precip (climate only)	6	39704.36	99.32	0.00	-19846.18
Inter comp + Intra comp (competition only)	6	40111.22	506.18	0.00	-20049.61
Total comp (competition only)	5	40144.15	539.10	0.00	-20067.07
Previous BAI + Tree (null model)	4	40188.08	583.04	0.00	-20090.04

Note: K is the number of parameters, Δ AIC is the difference from the top model, and AIC wt is the weight of each model.

Table 1.3. Top generalized linear mixed model for basal area increment (sugar pine growth). The top model with the lowest AIC included average January temperature of the current year (Jan temp), total precipitation from the previous fall (Fall precip), the interaction of temperature and precipitation (Jan temp * Fall precip), interspecific competition (Inter comp), and intraspecific competition (Intra comp).

Top growth model $R^2 = 0.81$ $RMSE = 9.96$					
Random effects	Variance	Standard deviation			
Tree (intercept)	0.0164	0.1281			
Residual	0.0561	0.2368			
Fixed effects	Coefficient estimate	Standard error	p-value	Standardized coefficient estimate (β)	VIF
Intercept	3.19918	0.05351	<0.0001	0	-
Jan temp	0.05394	0.00307	<0.0001	0.0041	2.9355
Fall precip	0.00028	0.00001	<0.0001	0.0025	1.3703
Jan temp * Fall precip	-0.00005	0.00001	<0.0001	-0.0017	3.0964
Inter	-0.13196	0.03	<0.0002	-0.0030	1.1001
Intra	-0.46277	0.07516	<0.0001	-0.0064	1.0902
Previous BAI	0.12436	0.00028	<0.0001	0.0122	1.0872

Note: R^2 is based off the relationship between actual and predicted values, RMSE is the root mean square error, and VIF is the variance inflation factor.

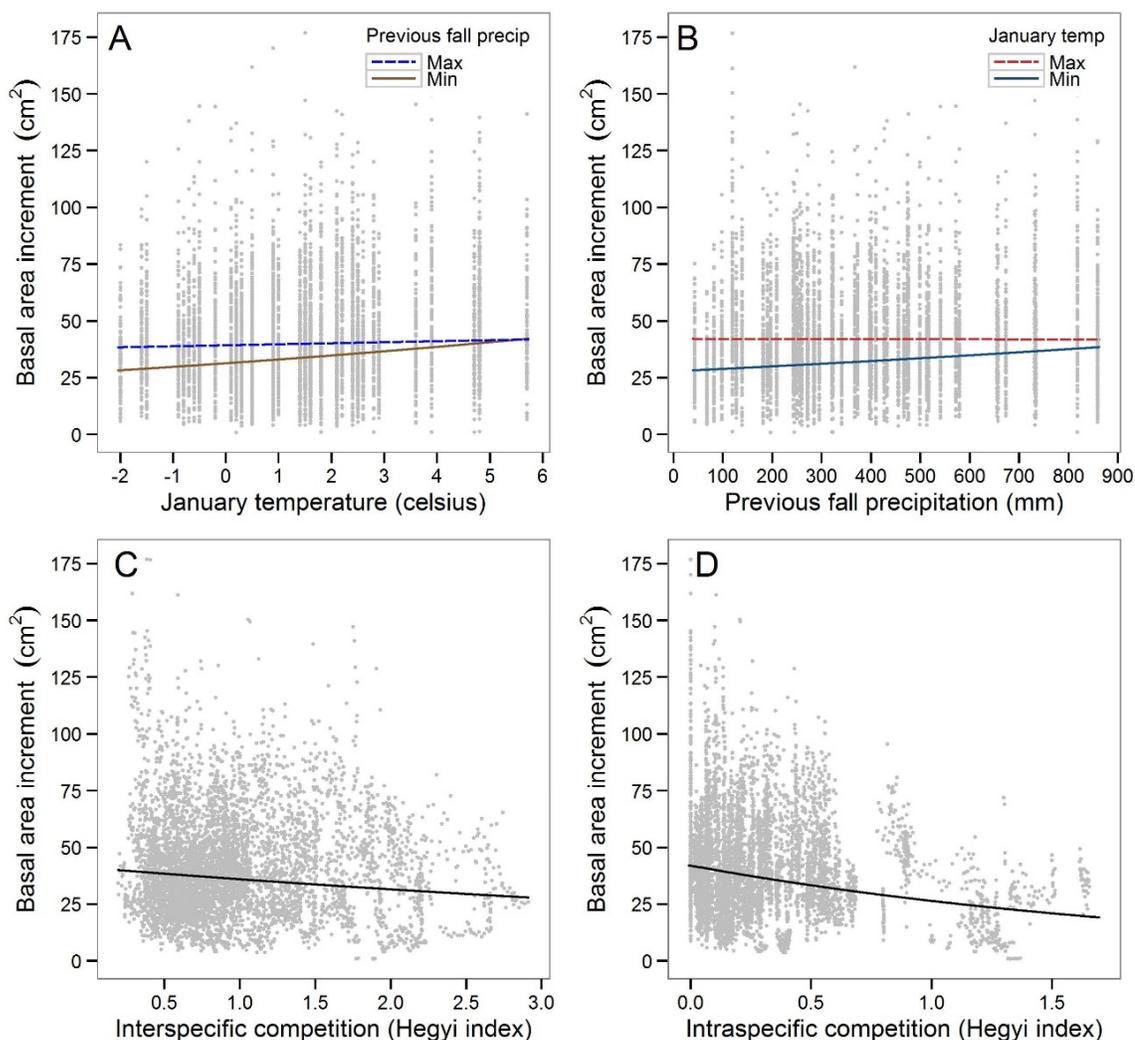


Figure 1.4. Scatterplots showing the relationship of basal area increment (BAI) with January temperature (A), previous fall precipitation (B), interspecific competition (C), and intraspecific competition (D). The two models in panel A represent the relationship between January temperature and BAI for maximum (dashed) and minimum (solid) total precipitation from the previous fall. The two models in panel B represent the relationship between previous fall precipitation and BAI for maximum (dashed) and minimum (solid) January temperature. Models are calculated using the coefficient estimates from the top model for BAI and represent the relationship for each predictor variable individually by taking the mean value for all other predictors.

The generalized linear mixed models that were most related to large sugar pine defense included measures of both climate and competition (Table 1.4). Models with measures of climate only or competition only had substantially higher AIC values (> 2) when compared to full models that incorporated both variable categories. Climate measures relating to water availability (e.g. climatic water deficit and precipitation) had a better association with defense than measures of temperature. In addition, defense was more strongly associated with total competition as opposed to subdividing competition into interspecific and intraspecific competition.

The top model for resin duct size included climatic water deficit, total precipitation (previous October – current April), and total competition (Table 1.5, Figure 1.5). The R^2 between predicted and actual values of resin duct size was 0.66, and the root mean squared error was 0.0224. Based on the standardized coefficient estimates, total competition had the strongest association with resin duct size ($\beta = -0.9571$). The standardized coefficient for climatic water deficit was -0.4085, and 0.2042 for total precipitation (Table 1.5). There were no interaction terms in the top model for resin duct size, however, the second and third best models were both < 2 AIC of the top model and included the interaction of total competition with total precipitation and climatic water deficit, respectively (Table 1.4). The coefficient estimate of the interaction between total competition and climatic water deficit ($\beta = 0.00004$) indicated that higher competition and higher climatic water deficit had a negative relationship with resin duct size.

Table 1.4. Generalized linear mixed models for resin duct size and total area (sugar pine defense). Predictor variables include climatic water deficit (WD), total precipitation from the previous October – current April (Precip), total competition (Total comp), average April temperature of the current year (April temp), average June temperature of the current year (June temp), interspecific competition (Inter), and intraspecific competition (Intra).

Model	K	AIC	Δ AIC	AIC Wt	Log Likelihood
Resin Duct Size					
WD + Precip + Total comp	7	-24252.91	0.00	0.35	12133.46
WD + Precip + Total comp + Precip * Total comp	8	-24252.11	0.80	0.23	12134.05
WD + Precip + Total comp + WD * Total comp	8	-24251.40	1.52	0.16	12133.70
WD + Precip + April temp + Total comp	8	-24251.28	1.63	0.15	12133.64
WD + Precip (climate only)	6	-24249.70	3.21	0.07	12130.85
WD + Precip + April temp (climate only)	7	-24248.47	4.44	0.04	12131.24
Total comp (competition only)	5	-24208.96	43.95	0.00	12109.48
Inter comp + Intra comp (competition only)	6	-24207.36	45.55	0.00	12109.68
BAI + Tree (null)	4	-24202.93	49.99	0.00	12105.46
Resin Duct Total Area					
WD + Precip + Total comp + June temp * Total	8	-3797.35	0.00	0.78	1906.68
Precip + June temp + Total comp + WD * Total comp	8	-3793.47	3.88	0.11	1904.74
WD + Jun temp + Precip + Total comp	8	-3792.78	4.57	0.08	1904.39
WD + Precip + Jun temp + Inter comp + Intra comp	7	-3790.79	6.56	0.03	1904.40
WD + Precip + Jun temp (climate only)	8	-3775.29	22.07	0.00	1894.64
WD * Jun temp + WD + Jun temp + Precip (climate only)	8	-3773.49	23.86	0.00	1894.75
Total comp (competition only)	5	-3753.81	43.54	0.00	1881.91
Inter comp + Intra comp (competition only)	6	-3752.91	44.44	0.00	1882.46
BAI + Tree (null)	4	-3740.18	57.18	0.00	1874.09

Note: K is the number of parameters, Δ AIC is the difference from the top model, and AIC wt is the weight of each model.

Table 1.5. Top generalized linear mixed model for resin duct size (sugar pine defense). The top model included climatic water deficit, total precipitation from the previous October- current April (Precipitation), and total competition (Total comp).

Resin duct size model $R^2 = 0.66$ $RMSE = 0.0224$					
Random effects	variance	Standard deviation			
Tree (intercept)	0.0129	0.1133			
Residual	0.0463	0.2153			
Fixed effects	Coefficient estimate	standard error	p-value	Standardized coefficient estimate (β)	VIF
Intercept	-2.27684	0.04629	<0.0001	0	-
Climatic water deficit	-0.00019	0.00004	<0.0001	-0.4085	1.3038
Precipitation	0.00002	0.00001	0.0208	0.2042	1.3083
Total comp	-0.052701	0.02323	0.0233	-0.9571	1.0578
BAI	0.001038	0.00024	<0.0003	0.6220	1.1081

Note: R^2 is based off the relationship between actual and predicted values, RMSE is the root mean square error, and VIF is the variance inflation factor.

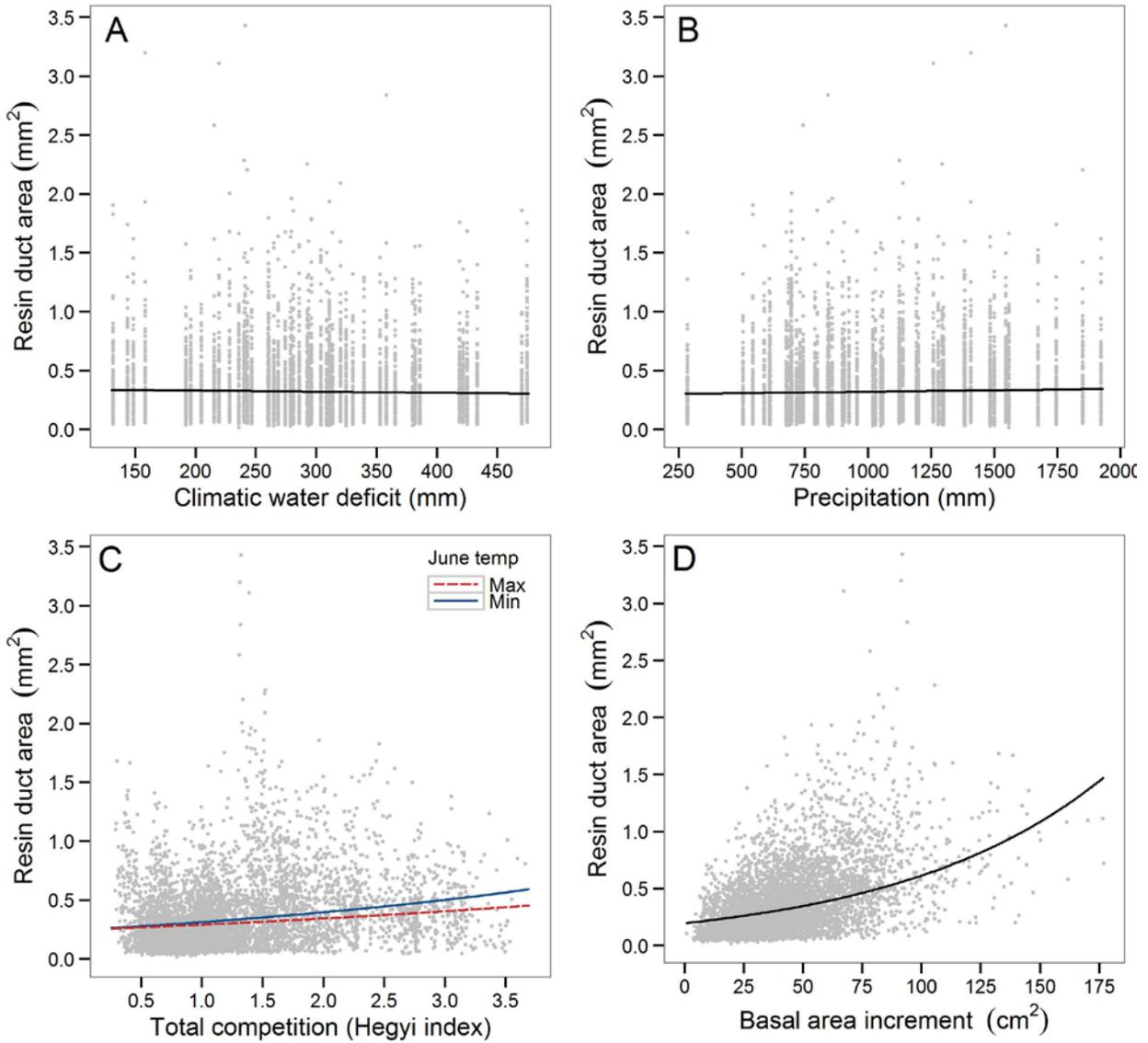


Figure 1.5. Scatterplots showing the relationship between resin duct size and climatic water deficit (A), total precipitation from the previous October – current April (B), total competition (C), and basal area increment as a covariate (D). Models are based on the top model for BAI and represent the relationship for each predictor variable individually.

Resin duct total area in large sugar pine had a stronger relationship with the model that included climatic water deficit, precipitation, total competition, and the interaction of June temperature with total competition (Table 1.6). The relationship between predicted and actual values of resin duct total area had an R^2 of 0.54, and a root mean squared error of 0.2108. Resin duct total area was most associated with total competition ($\beta = 0.8267$), and had a positive relationship where higher resin duct total area was related to higher competition. Total competition also showed an interaction with average June temperature, where higher June temperatures weakened the relationship between total competition and resin duct total area (Figure 6).

Table 1.6. Top generalized linear mixed model for resin duct total area (sugar pine defense). The top model included climatic water deficit, total precipitation from the previous October- current April (Precipitation), and total competition (Total comp), and the interaction between total competition and average June temperature of the current year (Total comp* June temp).

Resin duct total area model $R^2 = 0.54$ RMSE = 0.2108					
Random effects	Variance	Standard deviation			
Tree (intercept)	0.0483	0.2199			
Residual	0.2963	0.5443			
Fixed effects	Parameter Estimate	Standard error	p-value	Standardized estimate	VIF
Intercept	-1.88949	0.08523	<0.0001	-	-
Climatic water deficit	-0.00028	0.00011	<0.0130	-0.0734	1.4473
Precipitation	0.00007	0.00002	0.0023	0.0894	1.4194
Total comp* June temp	-0.012142	0.00315	<0.0001	-0.3906	2.2194
Total comp	0.37199	0.06253	<0.0001	0.8267	2.0866
BAI	0.001398	0.00063	0.0001	0.8361	1.1322

Note: R^2 is based off the relationship between actual and predicted values, RMSE is the root mean square error, and VIF is the variance inflation factor.

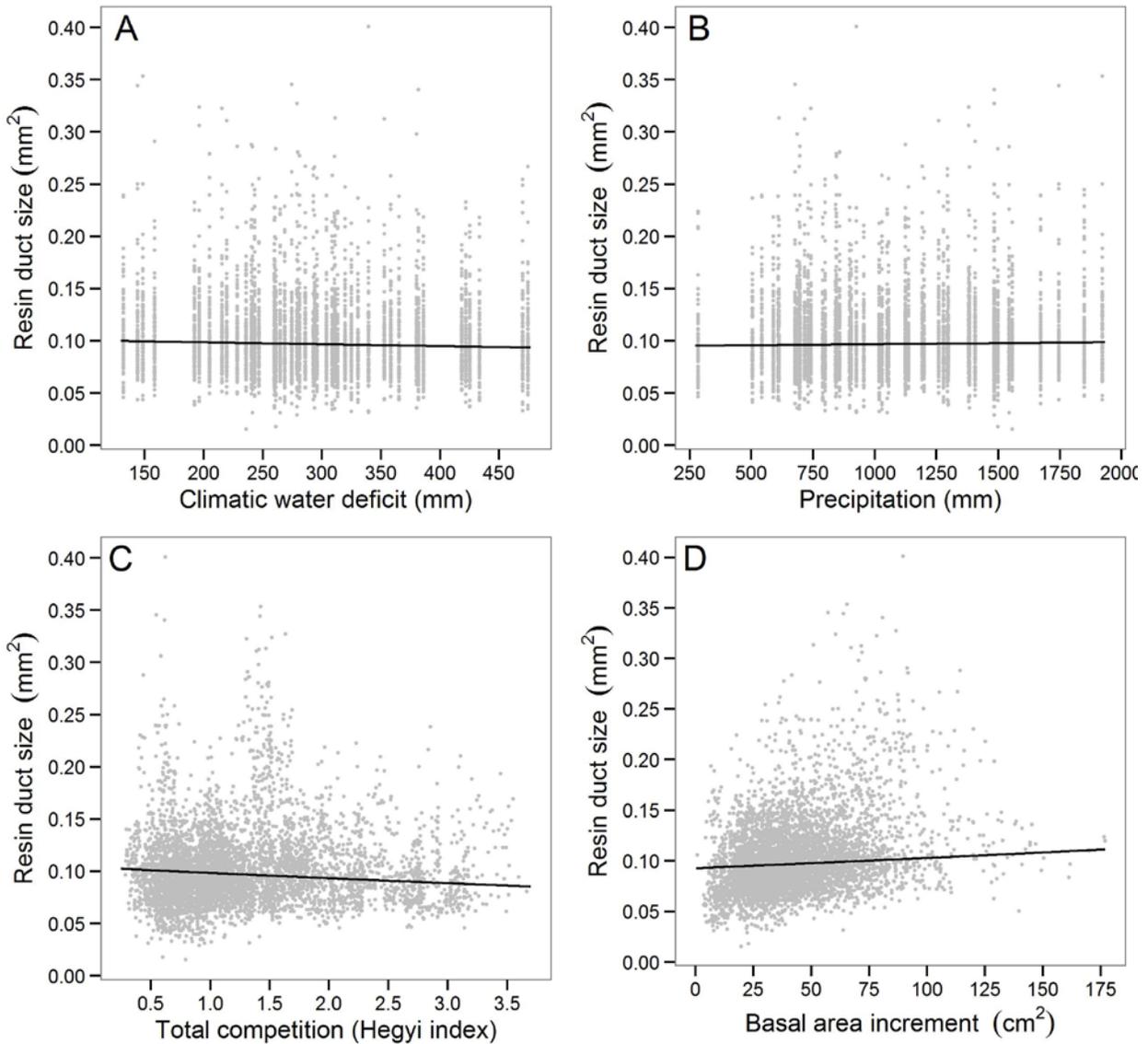


Figure 1.6. Scatterplots showing the relationship between resin duct size and climatic water deficit (A), total precipitation from the previous October – current April (B), total competition (C), and basal area increment as a covariate (D). The model for total competition displays the relationship with resin duct total area when June temperature was highest (Max) and lowest (Min). Models are based on the top model for BAI and represent the relationship for each predictor variable individually.

Discussion

The influence of climate and competition on growth

Large sugar pine at STEF have increased annual basal area increment since 1964, with most of the increase occurring after 1987 (Figure 3A). Increased growth may be driven by a combination of increased January temperature and decreased competition. Average January temperature at STEF has increased by $0.06^{\circ}\text{C y}^{-1}$ over the last 50 years, and mortality of competition trees in the last 10 years decreased average basal area by $0.012\text{ m}^2\text{ y}^{-1}$ for interspecific competition and by $0.014\text{ m}^2\text{ y}^{-1}$ for intraspecific competition. These findings are consistent with previous research that found increased growth with higher winter temperatures and lower competition for Scots pine (Sanchez-Salguero et al. 2015). For sugar pine, Das (2012) found declining growth rates with increasing competition. The standardized coefficient estimates indicated that increased growth in our study was most associated with lower intraspecific competition and may have a greater effect on growth than climate. Growth has also been shown to be more limited by competition than climate on the Iberian Peninsula (Gómez-Aparicio et al. 2011; Sanchez-Salguero et al. 2015), and competition was the primary driver of tree mortality, growth and recruitment in forests across Canada (Zhang et al. 2015).

The results show strong evidence (higher r and standardized estimate) that sugar pine growth was more associated with warmer January temperatures, than precipitation or climatic water deficit, suggesting that growth at STEF may have been limited by colder winter temperatures (i.e. limited by growing season) as opposed to being water limited. Similar relationships have been found in other conifers at high elevations in California (Bunn et al. 2005). However, this result is surprising considering the elevation of the study site was 1700 m.

Previous studies have suggested that the transition from low elevation, water limited forest to high elevation, temperature limited forests occurs somewhere between 2000 and 2600 m in the Sierra Nevada (Trujillo et al. 2012; Das et al. 2013). Large diameter sugar pine could be less water limited when compared to all species and size classes in the stand, because larger diameter trees can have greater access to ground water and larger canopies can capture more precipitation (Kerhoulas et al. 2013).

Large sugar pine growth was more limited by intraspecific competition than total or interspecific competition. This result was consistent with Das (2012), where intraspecific competition consistently had a stronger effect on growth for many conifer species, including sugar pine. Additionally, pines can be stronger competitors than shade tolerant species, such as white fir and incense cedar (Das 2012). Large sugar pine at STEF commonly occurred in clusters that likely had greater competition for light. Interspecific competition may have been less important because it mostly consisted of smaller incense cedar and white fir that likely did not compete as directly for aboveground and belowground resources. Competition dynamics for large sugar pine in the Sierra Nevada are complex, and the composition of competition matters when considering the impacts of growth.

The influence of climate and competition on defense

There is now increased evidence that resin duct defenses can be significantly influenced by climate (Hood et al. 2015, Slack et al. 2016), but the relationship of resin ducts with seasonal and monthly measures of climate can vary by species and geographic region. Total precipitation (previous October – current April) and climatic water deficit were associated with large sugar pine defense, and indicated that less water availability could have a significant impact on

reducing the ability of large sugar pine to defend against invading pests. Resin duct size was best associated with warmer April temperatures and total precipitation, while more total area was most correlated with June temperature and total precipitation. In another study resin duct total area in ponderosa pine was similarly greater when July temperatures were warmer (Hood et al. 2015), but was limited by July precipitation. Longleaf pine resin duct total area was lower following a dry winter and did not show a significant relationship with temperature (Slack et al. 2016).

To our knowledge this is the first study to examine the relationship between competition and resin duct defenses. Resin duct total area has remained relatively constant since 1964, and our results imply that resin duct total area does not respond to competition in the same way as resin duct size. Total competition had the greatest influence on resin duct total area, but the relationship was positive. This finding was surprising; however, more resin duct area can be influenced by both changes in size and production (i.e. count per year). For instance, resin duct production also had a positive relationship with total competition ($r = 0.29$; Slack unpublished data). Previous research has suggested that resin ducts may be induced under stress (Hood et al. 2015), and a more competitive environment may have increased production while decreasing size in large sugar pine. This result is consistent with the growth-differentiation balance hypothesis (GDBH), where greater competition may have limited resources, such as water and nutrients, enough to reduce growth. However, higher competition likely had less of an effect on photosynthesis because large diameter sugar pine were not light limited, increasing the availability of carbohydrates for allocation to resin duct defense (Herms and Mattson, 1992). The conflicting results imply that limiting factors associated with resin duct total area may be different than size, highlighting the importance of examining more than one measure of defense.

Future implications

Continued increases in temperature and climatic water deficit will likely have mixed effects on large sugar pine vigor due to differential impacts of climate on growth and defense. Climatic water deficit is expected to continue to rise by as much as 23% (from 2020-2049) due to increased temperature and decreased snowpack (Lutz et al. 2010), which could negatively impact resin duct defenses. However, growth could continue to increase in the future because winter temperatures are also expected to increase (Melillo et al. 2014).

In forests where fire exclusion continues to persist, competition patterns could have a contrasting influence on resin duct defense. Higher competition could limit resin duct size but increase resin duct total area by possibly inducing production. In areas where competition increases as a result of fire exclusion, large sugar pine may have a larger reservoir of resin (indicated by more resin duct total area) to pitch out invading pests. However, following Poiseuille's Law, resin flow through smaller ducts results in greater resistance and reduced flow by the fourth power (Schopmeyer et al. 1954).

Even if higher intraspecific competition limits sugar pine growth, slower growth may not increase overall tree vigor and the probability of mortality. For example large sugar pine mortality models indicate that a higher probability of mortality is associated a declining growth trend 10 years before tree death and not lower average growth (see Chapter 2). When preserving large sugar pine is the management objective, thinning treatments that reduce intraspecific competition may want to be prioritized in areas of declining growth rather than slower relative growth. Furthermore, large sugar pine mortality was also associated with declining resin duct total area 10 years before tree death (see Chapter 2). Results from this study suggest that resin duct total area is higher when competition is higher, and thinning treatments could have the

unintended consequence of reducing resin duct total area. Future forest treatments designed to increase forest resiliency could have both benefits and unintended consequences on large sugar pine vigor.

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CHAPTER 2: LARGE SUGAR PINE MORTALITY MODELS INFORMED BY GROWTH,
DEFENSE, AND COMPETITION IN A FIRE-EXCLUDED FOREST OF THE CENTRAL
SIERRA NEVADA

Abstract

Many old-growth pine forests across the western United States have encountered widespread and concerning increases in tree mortality. Due to past management practices and the negative impacts of fire exclusion, many forests that once experienced a high frequency and low intensity fire regime are now experiencing substantial competition and reduced vigor. These conditions could predispose individual trees to mortality, especially in forests where climate change is likely to increase the severity of drought. We investigated the importance of growth, resin duct defense, and competition on large sugar pine (*Pinus lambertiana*) mortality in a fire-excluded mixed-conifer forest of the Sierra Nevada. Basal area increment, resin duct size and total area, and basal area of competition were measured for 33 pairs of live and dead large diameter (> 50 cm) sugar pine at the Stanislaus-Tuolumne Experimental Forest in the central Sierra Nevada. Logistic regression analyses revealed that the best models for predicting large sugar pine mortality included measures of growth, defense, and competition; however, based on standardized coefficients growth measurements had the greatest effect. In general, shorter and recent time windows (10 and 5 years before mortality) were more informative than longer or past time windows. In the 10 years before mortality, basal area increment decreased in dead sugar pine ($-1.78 \text{ cm}^2 \text{ y}^{-1}$), but increased in live sugar pine ($0.34 \text{ cm}^2 \text{ y}^{-1}$; $p < 0.0001$), and growth variation was higher in live sugar pine than dead sugar pine ($p = 0.0016$). Resin duct total area decreased in dead sugar pine 10 years before mortality ($-0.0154 \text{ mm}^2 \text{ y}^{-1}$), but increased in live

sugar pine ($0.0068 \text{ mm}^2 \text{ y}^{-1}$, $p < 0.0001$). The top mortality model also included the slope of white fir competition during the 5 years before mortality, and the 50 year coefficient of variation for resin duct total area. The results from this study highlight that growth along with shorter and recent time windows were most associated with the probability of large sugar pine mortality.

Introduction

Older and larger pine species are highly valued for many ecological and ecosystem services, including critical wildlife habitat, long-term carbon sequestration, and ecosystem resiliency. However, old-growth forests are rare across most western U.S. landscapes and the persistence of these ecosystems is of great concern to land managers (Kolb et al. 2007). Due to past land management practices and shifting climates, many researchers have shown that background mortality rates and the occurrence of large scale die-off events in many forest ecosystems have been increasing in recent decades (van Mantgem et al. 2009; Allen et al. 2010; Smith et al. 2015). In particular, fire exclusion has dramatically altered the structure and composition in many old-growth pine forests. Historically, high frequency and low intensity fire regimes maintained more open stands. In the absence of fire many of these stands have become denser with a higher proportion of shade tolerant species (Nacify et al. 2010; Collins et al. 2011; McIntyre et al. 2015). As a result, older and larger trees are more prone to mortality than in the past due to uncharacteristically severe wildfire, pathogen and insect outbreaks, drought, and increased competition (Kolb et al. 2007; Bennett et al. 2015). Furthermore, the impacts of these disturbances and changes in forest structure are often exacerbated by the effects of climate change (Westerling et al. 2006, Raffa et al. 2008).

Fire-excluded forests are sometimes more susceptible to larger scale mortality events because the increase in competition can place added stress on individual trees (Savage 1997; Allen 2007). Understanding the mechanisms explaining tree mortality are difficult to identify because multiple factors occurring throughout a tree's lifespan can contribute to mortality (Waring 1987, Manion 1991). Tree growth and defense provide researchers the opportunity to

assess tree vigor over time because growth and defense respond to environmental changes (van Mantgem et al. 2003; Hood et al. 2015). Increasing competition can also contribute to mortality by limiting access to aboveground and belowground resources (e.g. light, water, and nutrients; Biging and Dobbertin 1992). By discerning the relative importance of specific factors, managers interested in protecting large pines and restoring old-growth forests will be equipped with the information to develop more effective and efficient management plans.

Many studies have related tree growth patterns to mortality, with most showing that slower annual growth is associated with a higher probability of mortality (Pederson 1998; Bigler and Bugmann 2003, 2004; Hanna and Kulakowski 2012; Kane and Kolb 2014). In addition to annual growth rate, other measures of growth have informed tree mortality models. 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 with less year-to-year growth variability (i.e. less sensitive) were more prone to mortality (Ogle 2000; Kane and Kolb 2014). Lastly, abrupt growth declines (substantial decreases in growth from one year to the next) may characterize prior events that contributed to mortality (Pederson 1998, Das et al. 2007). Previous research has found that the time period analyzed matters, but results have varied among studies. For instance, some studies found that tree mortality was related to shorter (≤ 10 year) time windows (Ogle et al. 2000; Bigler and Burgmann 2004; Hanna and Kulakowski 2012), while other studies linked tree mortality to longer (≥ 10 year) time windows (Pederson 1998; Bigler and Bugmann 2003; Das et al. 2007), or a combination of short- and long-term growth (Kane and Kolb 2014).

Evidence from recent research has also emphasized the importance of resin duct defenses in reducing susceptibility to bark beetle attack and subsequent mortality (Kane and Kolb 2010;

Gaylord et al. 2013; Ferrenberg et al. 2014; Hood et al. 2015). Resin ducts produced in the secondary xylem are important in defending many tree species against insect and pathogen attack because parenchyma cells within duct walls synthesize oleoresins that chemically impair, isolate and expel invading bark beetles (Franceschi et al. 2005). Vertical and radial resin ducts also create an extensive network that stores resin and allows resin to flow to the site of attack. Resin duct production has been linked to tree health (Paine et al. 1997), and offers a retrospective assessment of tree defense over time. Across the western United States, resistance to bark beetle attack in pines has been associated with vertical resin duct properties. For example, pinyon pine (*Pinus edulis*) in the southwest that survived bark beetle attack had larger resin ducts (Gaylord et al. 2013); in Colorado resistant limber pine (*Pinus flexilis*) and lodgepole pine (*Pinus contorta*) produced more resin ducts 5 and 10 years prior to bark beetle attack (Ferrenburg et al. 2014); and resin ducts in resistant ponderosa pine (*Pinus ponderosa*) were larger and had more total area (Hood et al. 2015). Including measures of resin duct defenses have also been shown to more accurately predict mortality when compared to growth during a bark beetle outbreak for ponderosa pine in the southwest U.S. (Kane and Kolb 2010). Incorporating measures of both growth and defense in prediction models could offer a more complete assessment of factors related to pine mortality.

Competition is also a potentially important contributor to tree mortality and has been widely studied for conifers in North America. Generally, higher competition often leads to an increased probability of mortality (Temesgen and Mitchell 2005; Das et al. 2008, 2011), but results have not been consistent and there is still disagreement about the role of stem density on mortality (Meddens et al. 2015). As forests age, insects and pathogens play a greater role in large tree mortality, but competition may still influence mortality patterns when biotic agents only kill

individual trees with the greatest levels of competition (Das et al. 2011). Including spatial elements of competition can provide additional information on the effects on tree stress than growth measures alone. For instance, Das et al. (2008) found that including competition improved mortality models. Finally, when examining the effects of fire exclusion it is important to quantify measures of competition over time, and to examine the relationship between trends in competition with large tree mortality. We are only aware of one study that used a retrospective competition index to examine the role of drought on competition for pubescent oak (*Quercus pubescens*) and Scots pine (*Pinus sylvestris*) (Webber et al. 2008).

Our study examined large sugar pine (*Pinus lambertiana*) in the central Sierra Nevada because many old-growth forests with a sugar pine component currently have an elevated mortality risk, in part due to changes in stand structure and composition (van Mantgem et al. 2004). High frequency and low intensity fire regimes, that were once common in the Sierra Nevada, maintained relatively open but heterogeneous stands of old-growth, mixed-conifer and limited ingrowth from shade tolerant species. However, a century of fire exclusion has increased tree density leading to greater competition that has potentially placed added stress on large trees (Smith et al. 2005; Knapp et al. 2013; McIntyre et al. 2015). Greater competition could predispose large sugar pine to increased mortality from various disturbances and the effects of climate change could exacerbate mortality trends (Miller and Urban 1999, Battles et al. 2008). Furthermore, due to fire exclusion and past logging activities, stand structure has shifted to smaller diameter classes, and larger trees, including sugar pine, are underrepresented (Lutz et al. 2009; Knapp et al. 2013). For these reasons there is substantial interest in preserving large sugar pine in remnant old-growth stands and restoring previously logged mixed-conifer forests in the Sierra Nevada.

Growth and competition have been relatively well studied for sugar pine (Das et al. 2007, 2008, 2011; Das 2012; Nesmith et al. 2015; Das and Stephenson 2015), but there is no research examining the role of defense or comparing the relative importance of all three variables. In addition, we included a retrospectively reconstructed estimate of competition to better understand how trends in competition may influence the probability of sugar pine mortality. The main objective of this study was to determine the relative importance of growth, defense, and competition in predicting the probability of large sugar pine mortality in a fire-excluded, mixed-conifer forest of the central Sierra Nevada. We also examined varying time windows to determine the role temporal scale within measures of growth and defense on large sugar pine mortality. Specifically, we addressed the following research questions:

- 1) What are the differences in measures of growth, defense, and competition between live and dead sugar pine?
- 2) What variables and time frames of growth, defense, and competition are most closely associated with the probability of sugar pine mortality?

Methods

Study area

The study was completed in the Stanislaus-Tuolumne Experimental Forest (STEF; 38°10'N, 120°00'W; Figure 1.1) near Pinecrest, California. The study site covered about 55 hectares of mid-elevation (1585 to 1890 m), mixed-conifer forest type, commonly found on the western slopes of the Sierra Nevada. Climate consisted of warm dry summers and cold wet winters, with a majority of precipitation falling as snow during winter months (Knapp et al. 2013). Subject sugar pine trees were located mid-slope on north to northwest aspects with slopes ranging from 2-18°. Soils were loam to gravelly loam of the Wintoner-Inville families complex, formed primarily from granite, creating a deep, well-drained, and highly productive site. Historical data showed that in 1929 adjacent stands were dominated by white fir (*Abies concolor*), sugar pine, incense cedar (*Calocedrus decurrens*), ponderosa pine, and Jeffrey pine (*Pinus jeffreyi*), in order of abundance (Knapp et al. 2013).

The historical fire regime of STEF had a median return interval between 5 and 8 years, but the stand has not experienced a fire since 1889 (Knapp et al. 2013). In the absence of fire, shade-tolerant white fir and incense cedar have increased in abundance with proportionally less pine (Knapp et al. 2013). In 2012, a thinning treatment was applied to approximately 80% of the study area that mostly removed smaller diameter trees and retained larger overstory trees. Prior to the 2102 treatment, the study area was mostly unlogged. A few stumps existed, but were likely a result of sanitation salvage that removed dead and dying trees to reduce the population and spread of bark beetles. Mortality in the largest diameter classes was low, and there was no evidence of recent epidemic bark beetle outbreaks at the site.

Data collection

We selected all large standing dead sugar pine within the study site that produced a viable tree core as subject trees, and avoided sampling dead trees that experienced mechanical failure. Diameter at breast height (DBH) for all subject trees ranged from 52 cm to 168 cm. All dead sugar pine showed at least one sign or symptom of bark beetle activity, including exit holes, galleries inside the bark, and associated fungal species (e.g., *Ophiostoma* spp., *Cryptoporus* spp.). A total of eight sampled dead sugar pine showed signs of rhizomorphs at the base of the tree, indicating the presence of the root disease caused by *Armillaria* spp. Each dead tree was then paired with the closest live tree based on close proximity (within 100 m) and similar DBH (± 5 cm). The paired design limited differences in soils, topographic features, and other microsite conditions. A total of 33 pairs of live and dead sugar pine were sampled ($n = 66$).

For all sampled sugar pine we recorded DBH and bark thickness; extracted one large diameter (12 mm) and one narrow diameter (5 mm) core at breast height (1.37 cm) with an increment borer to measure growth and defense variables for each tree. To measure the competition surrounding each sugar pine, a nested, fixed-area plot was established with the subject tree as the plot center. We included all competitor trees taller than breast height within 5 m of plot center, all trees with a DBH greater than 5 cm within 10 m, and large diameter trees with a DBH greater than 50 cm within 20 m (Figure 1.2). For each competitor tree we recorded species, DBH, basal diameter, status (live, dead, cut), distance to subject tree, and azimuth to subject tree. For all standing dead trees we recorded decay class, which was modified from a previous study (Imbeau and Desrochers 2002) to only include categories for dead trees (snags). A total of 586 uncut competitor trees (10.1% of all measured competitor trees) were cored to the pith (tree center) at breast height using a small diameter (5 mm) increment borer for the purpose

of retrospectively estimating competition. The cored competition trees represented the species composition of the whole study area, and included 222 white fir (19 dead), 137 incense cedar (20 dead), 147 sugar pine (13 dead), 41 Jeffrey pine, 38 ponderosa pine, 1 California black oak (*Quercus kelloggii*), and 1 mountain maple (*Acer glabrum*).

Growth, defense, and competition measures

All tree cores were mounted and progressively sanded with 80- to 600- grit sand paper, then scanned to create a high resolution (1,200 dpi) image. Each image was analyzed in the program WinDendro (Regent Instruments 2014), where annual ring boundaries were assigned and total ring width (mm y^{-1}) was measured. All cores were visually crossdated 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 sugar pine from another study (see Chapter 1). The chronology for all 66 sugar pine trees had a series intercorrelation of 0.479 and a mean sensitivity of 0.174. Based on crossdating with the master chronology, all sampled sugar pine died between 1990 and 2013 with a majority (24 of 33) dying between 2000 and 2010.

Sugar pine growth was calculated as basal area increment (BAI, $\text{cm}^2 \text{y}^{-1}$):

Equation 1:
$$BAI_t = \pi(R^2 - r^2)$$

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

related growth trends while still maintaining suppression or release events that may be related to changes in climate or competition (Biondi and Qeadan 2008, Speer 2010). Sugar pine defense was estimated through measurements of vertical resin ducts within each annual tree ring. Resin ducts were identified and measured from high resolution images of each core using the program ImageJ (Rasband 2014). Annual measurements included the count of identified resin ducts (production, # ducts y^{-1}), mean resin duct size (size, $mm^2 y^{-1}$), the sum of resin duct total area (total area, $mm^2 y^{-1}$).

To examine the influence of competition, we retrospectively reconstructed competition by estimating the diameter inside bark for every individual competition tree going back in time. First, to account for the thinning treatment that occurred in 2012, we measured the basal diameter for all live trees and built site-specific regression models for each species to estimate the 2014 DBH for all cut competition trees (Appendix A). All trees cut in 2012 were assumed to be living at the time of treatment. Site- and species-specific bark thickness equations were then constructed (Appendix A) to estimate the bark thickness for all competitor trees that were not cored to determine the diameter inside bark for the last year of growth. The last year of growth was estimated for each standing dead competitor by constructing species-specific equations based on the relationship between the last year of growth in cored samples and associated decay class (Appendix A). We could not extract viable cores from dead trees that had fallen, and fallen trees may have influenced competition during the time period analyzed, possibly increasing the uncertainty of earlier competition estimates.

Once the diameter inside bark (DIB) during the last year of growth was determined for all competitor trees, mean ring widths were then progressively subtracted to estimate DIB for each year. Mean ring width for each year was estimated by species and tree size using the 585

collected competition cores. Analysis of variance showed that mean growth was not statistically different among size classes for incense cedar, sugar pine, Jeffrey pine, and ponderosa pine, but was different between three size classes for white fir. Competition was calculated using the distance-dependent Hegyi index and the sum of the basal area of all competitor trees. However, preliminary analysis showed that large sugar pine mortality was best explained by the basal area of competition and the Hegyi index was dropped from analysis. The equation for the basal area of competition was:

$$\text{Equation 2: } BA_t = \sum_{j=1}^n 0.00007854 \times DIB_{jt}^2$$

Where BA_t is basal area in year t and DIB_{jt} was the diameter inside bark for competitor tree j in year t . Estimations for competition were subdivided into interspecific competition (i.e. non-sugar pine competitors), intraspecific competition (i.e. sugar pine competitors), white fir competition, and total competition.

Measures of sugar pine growth and defense were calculated as averages, year-to-year variability (i.e. coefficient of variation, COV), and trends over time (i.e. slope). For each pair of live and dead sugar pine the 50 years before last year of growth in the dead tree was analyzed. This allowed for a large enough time frame to compare short-term (5 and 10 years) and long-term (25 and 50 years) time windows. Additionally, we examined past time windows (starting 50 years before tree death) and recent time windows (ending the year before tree death). For example, the recent 10 year average of BAI was the average BAI during the 10 years before tree death, and the past 10 year average of BAI was the average of BAI starting 50 years before tree death and ending 40 years before tree death. Abrupt growth declines were identified when BAI was 50% or less 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. Estimates for competition included the basal area of competition in the year before tree death, and the slope of competition basal area during the 5 years before tree death. We did not calculate variability because year-to-year changes in competition were subtle, and we did not include past trends in competition because of a higher uncertainty in competition estimates that were further back in time.

Statistical analyses

We used paired t-tests to examine the differences between live and dead sugar pine. When the assumption that the difference between pairs follows a normal distribution was not met the differences between live and dead sugar pine were analyzed using the non-parametric Wilcoxon signed-rank test. Results from the t-tests and Wilcoxon signed rank tests informed the selection of variables to be used in constructing sugar pine mortality models, where variables with high p-values were excluded from further analysis.

Logistic regression was used to model the probability of mortality using the package glm2 (Marschner 2014) in the statistical program R (R Development Core Team 2015). This statistical analysis estimates the probability of a binary response (i.e. live or dead) based on multiple predictor variables using the standard logistic function and the following equation:

$$\text{Equation 3: } P_m = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_m x_m)}}$$

Where P_m is the probability of mortality, β_0 is the intercept estimate, and $\beta_1 x_1$ is the coefficient estimate for variable 1. To avoid issues of multicollinearity, highly correlated predictor variables were not included in the same model and were verified based on a variance inflation factor (VIF) less than 10 (Burnham and Anderson 1998). Potential models included predictors for growth only, defense only, and competition only to examine how mortality is associated with each

variable separately. We then included models combining two variable categories, and combinations with all three to determine if combining variable categories together improved mortality models. In all, we built and analyzed 64 models and reported the top models with all variable categories, the top models combining two of the three variable categories (e.g. growth and defense) and the top model for each single category.

The top model was selected using Akaike's Information Criterion (AICc) with a correction factor to better estimate model performance when limited by a small sample size. Meaningful differences between models were indicated by a difference in AICc values greater than 2 (Burnham and Anderson 1998). To provide an estimate of model accuracy we calculated the area under the receiver operator characteristic curve (AUC). In addition, each model was validated internally by determining the percentage of correctly classified trees. We used a 0.5 cut-point threshold for determining mortality status from the probability of survival response of the logistic model, where a tree was predicted to be dead when the probability of survival ≤ 0.5 , and live trees had a probability of survival > 0.5 . Within the top model we calculated the standardized coefficient estimates post-hoc to inform the weight of each variable on large sugar pine mortality and interpret the relative importance of growth, defense, and competition:

$$\text{Equation 4: } \beta_{s1} = \beta_1 \times \frac{s_1}{s_y}$$

Where 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

Live and dead sugar pine had noticeable differences in growth, especially during shorter and recent time windows of 5 and 10 years (Table 2.1). The slope of BAI was on average negative for dead trees and positive for live trees during the 5, 10, and 25 years before tree death. The greatest difference in the slope of BAI occurred during the 10 year time window when dead trees decreased growth by $1.78 \text{ cm}^2 \text{ y}^{-1}$ and live trees increased growth by $0.34 \text{ cm}^2 \text{ y}^{-1}$ ($p < 0.0001$, Figure 2.1). There was a difference in the coefficient of variation, where year-to-year growth in dead trees was less variable than in live trees during the 10 years before tree death ($p = 0.0016$). In the last 5 years before tree death live trees became less variable and had a lower coefficient of variation than dead trees ($p = 0.0045$). Average basal area increment between live and dead trees showed no significant differences during recent time windows. However, when analyzing past time windows dead sugar pine did show a significant difference in average BAI, where dead trees grew 27% more than live trees (Figure 2.1). For example, average BAI during the past 25 year time window (i.e. the first 25 years of the 50 years analyzed) was $40.71 \text{ cm}^2 \text{ y}^{-1}$ for dead trees and $32.09 \text{ cm}^2 \text{ y}^{-1}$ for live trees ($p = 0.0149$).

Table 2.1. Comparison of growth variables between live and dead sugar pines. Growth was measured as basal area increment. Significant differences between live and dead sugar pine are based on paired t-tests or Wilcoxon signed-rank tests and are highlighted by an asterisk.

Basal area increment (cm²)	Live mean	Dead mean	Mean of differences	p-value
5 year time window				
Average	37.95 (3.22)	33.86 (3.66)	-4.1	0.4008
Slope	1.09 (0.65)	-0.86 (0.56)	-1.95	0.0370* ^w
COV	0.17 (0.01)	0.23 (0.02)	0.06	0.0045*
10 year time window				
Average	37.02 (3.03)	38.38 (4.14)	1.36	0.7902
Slope	0.34 (0.23)	-1.78 (0.49)	-2.12	<0.0001* ^w
COV	0.28 (0.02)	0.21 (0.02)	-0.07	0.0016* ^w
25 year time window				
Average	34.87 (2.66)	39.97 (3.89)	5.10	0.2790
Slope	0.34 (0.10)	-0.18 (0.15)	-0.52	0.0161* ^w
COV	0.30 (0.02)	0.25 (0.02)	-0.05	0.0800
50 year time window				
Average	33.48 (2.38)	40.34 (3.69)	6.86	0.0814
Slope	0.11 (0.06)	-0.06 (0.08)	-0.18	0.0819
COV	0.28 (0.02)	0.29 (0.02)	0.01	0.6879

^w Differences between live and dead sugar pine were tested using Wilcoxon signed-rank test.

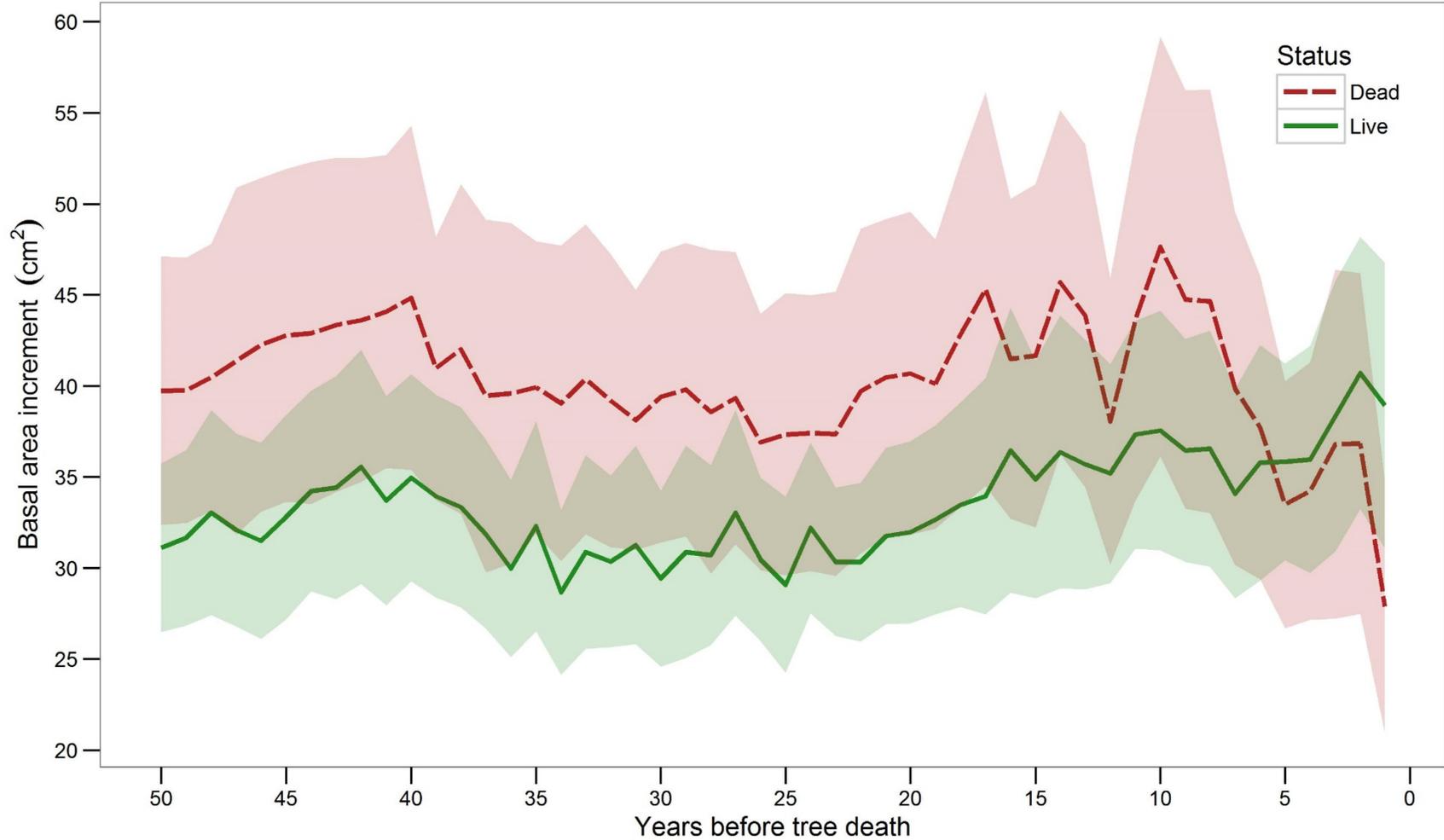


Figure 2.1. Mean growth (basal area increment) for dead (red) and live (green) sugar pine 50 years prior to tree death. Dead sugar pine experienced steep declines in growth 10 years before mortality, while live sugar pine concurrently increased growth. The first sugar pine died in 1991, and 24 of the 33 samples died between 2000 and 2010. The shaded bars represent the 95% confidence intervals.

Resin duct total area in dead sugar pine was lower than live sugar pine and showed declining trends during recent time windows (Table 2). Resin ducts in dead trees had 29% lower total area during the recent 5 year average ($p = 0.0276$, Figure 2.2). The greatest difference in the slope of resin duct total area occurred during the 10 year time window when resin duct total area in dead sugar pine decreased at an annual rate of $0.0154 \text{ mm}^2 \text{ y}^{-1}$ while live sugar pine increased total area by $0.0068 \text{ m}^2 \text{ y}^{-1}$. In general, year-to-year changes in resin duct total area showed a trend towards greater variability in live sugar pine, although none of the differences were statistically significant. Finally, there were no significant differences between live and dead sugar pine for recent and past estimates of resin duct production or size. However, during the 50 years analyzed mean resin duct size was 0.0846 mm^2 in dead sugar pine and 0.0923 mm^2 in live sugar pine ($p = 0.1244$).

The only statistical difference in competition between live and dead sugar pine was for intraspecific competition the year before tree death, where the basal area of competing sugar pine was 32% lower around dead trees than live trees ($p = 0.0106$; Table 2.3; Figure 2.3A). On average the basal area of total competition around dead sugar pine was 0.56 m^2 lower than live sugar pine, and interspecific competition for dead trees was only 0.14 m^2 higher than live trees. In general, the slope of competition basal area decreased around both live and dead sugar pine during the 5 years before tree death. For example, the basal area of white fir competition decreased at an annual rate of $0.0238 \text{ m}^2 \text{ y}^{-1}$ around live sugar pine and $0.0043 \text{ m}^2 \text{ y}^{-1}$ around dead sugar pine (Figure 2.3B).

Table 2.2 Comparison of resin duct defense variables, measures as total area, between live and dead sugar pines. Significant differences between live and dead sugar pine are based on paired t-tests and are highlighted by an asterisk.

Resin duct total area (mm²)	Live mean (SE)	Dead mean (SE)	Mean of differences	p-value
5 year time window				
Average	0.3369 (0.0415)	0.2382 (0.0206)	-0.0987	0.0276*
Slope	0.0185 (0.0112)	-0.0246 (0.0095)	-0.0431	0.0097*
COV	0.6939 (0.0777)	0.7139 (0.0694)	0.0200	0.7775
10 year time window				
Average	0.3197 (0.0372)	0.2749 (0.0200)	-0.0448	0.2681
Slope	0.0068 (0.0031)	-0.0154 (0.0043)	-0.0223	<0.0001*
COV	0.6564 (0.0602)	0.6432 (0.0371)	-0.0132	0.8391
25 year time window				
Average	0.3183 (0.0335)	0.2911 (0.0196)	-0.0272	0.4634
Slope	0.0012 (0.0015)	-0.0021 (0.0014)	-0.0033	0.0426*
COV	0.6858 (0.0434)	0.6121 (0.0251)	-0.0737	0.1357
50 year time window				
Average	0.3073 (0.0276)	0.2946 (0.0192)	-0.0127	0.6443
Slope	0.0007 (0.0007)	-0.0005 (0.0006)	-0.0012	0.2170
COV	0.6927 (0.0439)	0.6019 (0.0240)	-0.0908	0.0606

^w Differences between live and dead sugar pine were tested using Wilcoxon signed-rank test

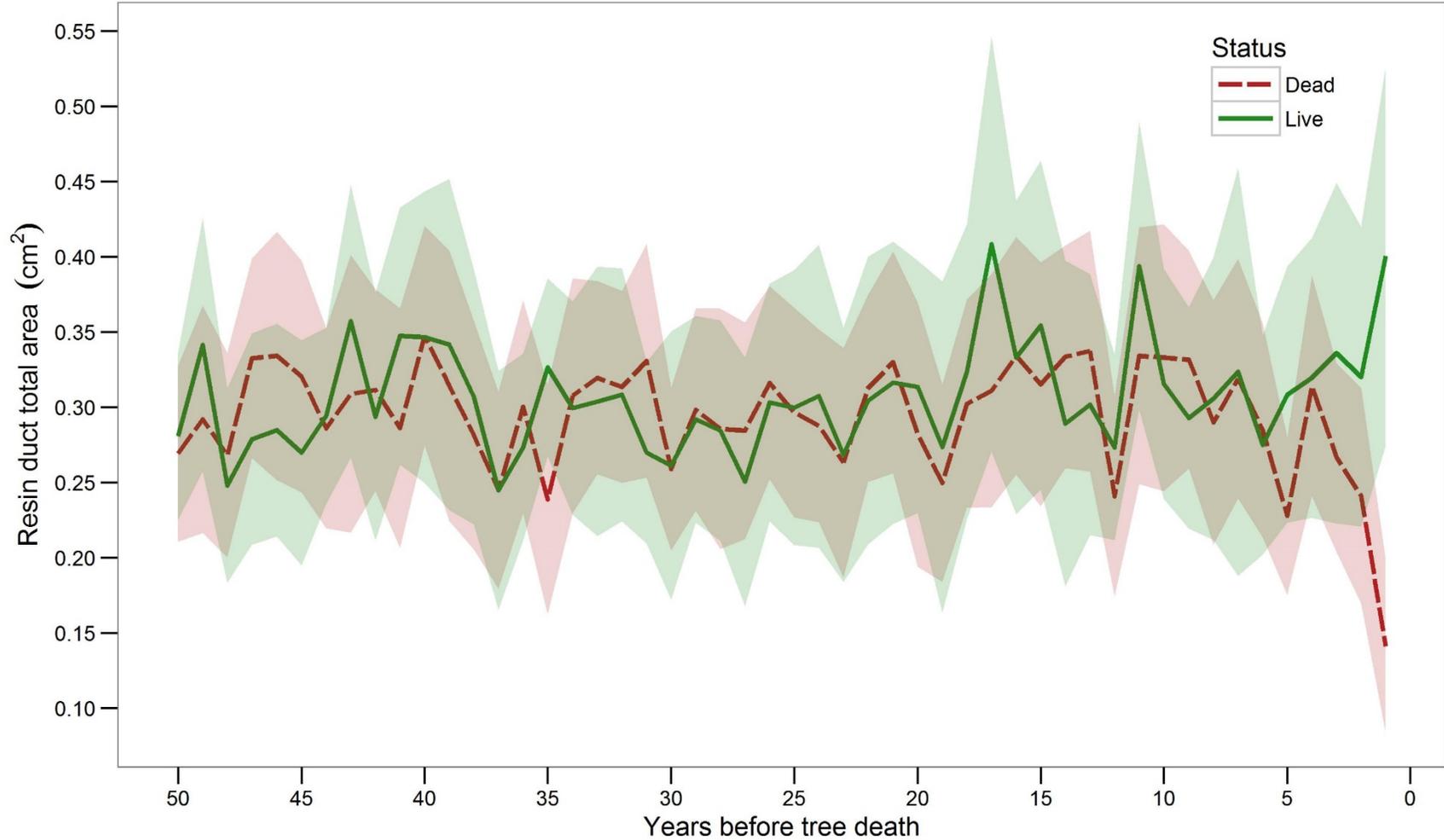


Figure 2.2. Mean resin duct total area for dead (red) and live (green) sugar pine 50 years before tree death. Years before tree death are based on the year of mortality for the dead tree within each pair of live and dead sugar pine. Shaded error bars represent the 95% confidence interval. The slope of resin duct total area during the 10 years before tree death was significantly lower in dead sugar pine, where resin duct total area in dead sugar pine decreased and increased live sugar pine.

Table 2.3 Comparison of competition variables between live and dead sugar pines. Competition was measured as basal area. Significant differences between live and dead sugar pine are based on paired t-tests and are highlighted by an asterisk.

Competition basal area (m ²)	Live mean (SE)	Dead mean (SE)	Mean of differences	p-value
Total				
Last year	5.21 (0.38)	4.65 (0.31)	-0.56	0.1972
5 year Slope	-0.0363 (0.0243)	-0.0013 (0.0083)	0.0350	0.5021 ^w
Interspecific				
Last year	2.96 (0.26)	3.14 (0.27)	0.18	0.6151
5 year Slope	-0.0193 (0.0151)	-0.0041 (0.0078)	0.0153	0.7111 ^w
Intraspecific				
Last year	2.28 (0.26)	1.56 (0.21)	-0.72	0.0106*
5 year Slope	-0.0170 (0.0211)	0.0028 (0.0038)	0.0198	0.5021 ^w
White fir				
Last year	1.67 (0.20)	1.81 (0.20)	0.14	0.5992
5 year Slope	-0.0238 (0.0153)	-0.0043 (0.0075)	0.0194	0.2075 ^w

^w Differences between live and dead sugar pine were tested using Wilcoxon signed-rank test

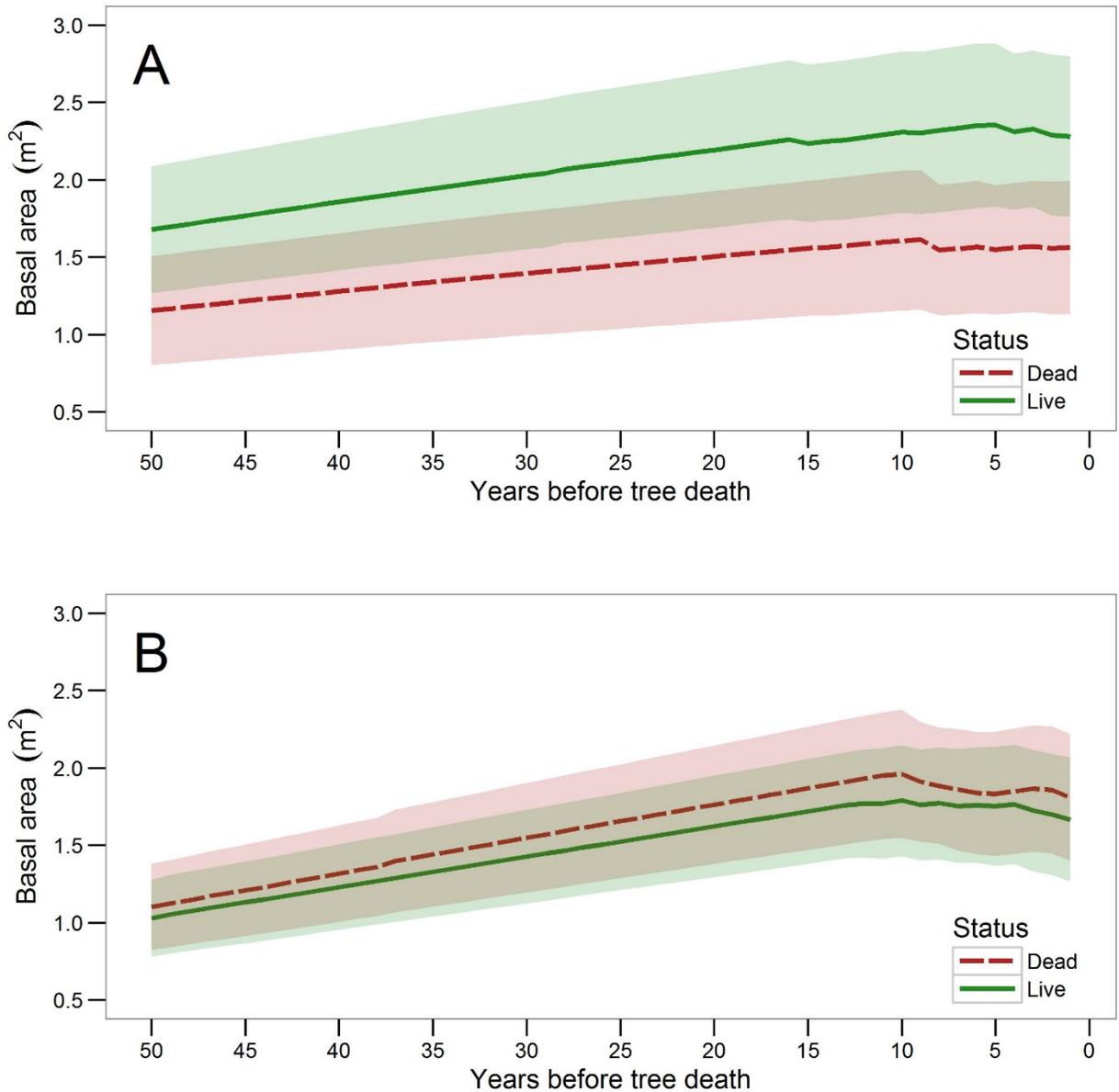


Figure 2. 3. Changes in intraspecific competition (A) and white fir competition (B) for dead (red) and live (green) sugar pine. Competitive load was measured as basal area for competition with other sugar pine (intraspecific, solid line) and competition with white fir (dashed line). At the time of mortality dead sugar pine had 32% less basal area of intraspecific competition when compared to live sugar pine. The slope of change in white fir basal area was also higher in dead sugar pine in the 5 years before tree death. Shaded error bars represent the 95% confidence interval.

Large sugar pine mortality models

The models with the lowest AICc for predicting tree mortality all included measures of sugar pine growth, defense, and competition (Table 4). Three models were within 2 AICc of the top model and all 4 of these models included the 10 year slope of BAI, the 10 year coefficient of variation of BAI, and the 5 year slope of white fir competition. At least one defense variable was in the top 4 models, and included the 10 year slope, the 50 year coefficient of variation, and the 5 year average of resin duct total area. All variables associated with large sugar pine mortality were during recent time windows, and no past time windows were included in the top models. With the exception of the 50 year coefficient of variation for resin duct total area, the top models favored short time windows (5 and 10 years) over long time windows (25 and 50 years). All models within 2 AICc of the top model had AUC values between 0.91 and 0.93, and correctly classified 83.3 to 89.3% of all trees (Table 4).

When comparing models that exclusively included growth, defense, or competition, the growth only model had the lowest AICc of 62.39 and the area under the receiver operator characteristic curve (AUC) was 0.88. The defense only model with the lowest AICc (AICc = 76.89, AUC = 0.79) performed better than all models of competition only (AICc = 90.29, AUC = 0.68). Models were improved when combinations of variable categories were included. For example, the growth only model correctly classified 77.3% of all trees, and adding the 5 year slope of white fir basal area to the growth model (AICc = 60.14, AUC = 0.90) correctly classified 80.3% of all trees.

The top model for predicting the probability of sugar pine mortality included the 10 year slope of BAI and resin duct size, the 5 year coefficient of variation for BAI, the 10 year slope of resin duct total area, the 50 year coefficient of variation for resin duct size, and the 5 year slope

of white fir competition (Table 5). The top model had an area under the receiver operator curve of 0.93, and correctly classified 84.8% of dead sugar pine, 81.8% of live sugar pine, and 83.3% of all trees. The standardized coefficient estimate was greatest for the 10 year slope of BAI (7.58), and lowest for the 50 year coefficient of variation for resin duct size (1.31).

Table 2.4. Summary of sugar pine mortality models. All models were built using logistic regression and the top model was selected using Akaike's information criterion with a correction for finite samples sizes (AICc).

Mortality models	Model type	K	AICc	Δ AICc	AICc wt	Log Likelihood	ROC	Trees correctly classified (%)		
								Dead	Live	Total
BAI slope10 + BAI COV10 + RD total area slope10 + RD total area COV50 + BA abco slope5	All	6	57.36	0.00	0.35	-21.97	0.93	87.9	84.8	86.3
BAI slope10 + BAI COV10 + RD total area slope10 + BA abco slope5	All	5	58.21	0.85	0.23	-23.60	0.92	84.8	81.8	83.3
BAI slope10 + BAI COV10 + RD total area COV50 + BA abco slope5	All	5	59.26	1.90	0.13	-24.13	0.91	81.8	87.9	84.8
BAI slope10 + BAI COV10 + RD total area slope10 + RD total area COV50 + RD total area average5 + BA abco slope5	All	7	59.32	1.96	0.13	-21.70	0.94	87.9	90.9	89.3
BAI slope10 + BAI COV10 + BA abco slope5	Growth and competition	4	60.14	2.78	0.09	-25.74	0.90	81.8	78.8	80.3
BAI slope10 + BAI COV10 + RD total area slope10 + RD total area COV50	Growth and Defense	5	61.26	3.90	0.05	-25.13	0.90	78.8	75.8	77.3
BAI slope10 + BAI COV10	Growth only	3	62.39	5.02	0.03	-28.00	0.88	72.7	81.8	77.3
RD total area slope10 + BA intra + BA abco slope5	Defense and competition	4	76.61	19.25	0.00	-33.98	0.82	78.8	72.7	75.8
RD total area slope10 + RD total area COV50	Defense only	3	78.65	21.29	0.00	-36.13	0.77	69.7	66.7	68.2
BA intra + BA abco slope5	Competition only	3	90.29	32.92	0.00	-41.95	0.68	69.7	60.6	65.2

Note: Prediction variables include: the 10 year slope of BAI (BAI slope 10), the 10 year BAI coefficient of variation (BAI COV10), the 10 year slope of resin duct total area (RD total area slope 10), the 50 year resin duct size coefficient of variation (RD size COV 50), the 5 year average of resin duct total area (RD total area average5), the 5 year average of resin duct size (RD size average5), the 5 year slope of white fir basal area (BA abco slope 5), and the competitive load of intraspecific competition in basal area (BA intra). K is the number of parameters, Δ AICc is the difference from the top model, AICc wt is the weight of each model, and ROC is the area is the receiver operator curve.

Table 2.5. Prediction variables for the top logistic regression mortality model. The standardized coefficient was calculated post-hoc in terms of standard deviation, and offers an estimate of the strength of the effect of each variable.

Predictor	Coefficient estimate	Standard error	p-value	Standardized coefficient	VIF
Intercept	-5.83	2.17	0.0071	0	-
BAI slope 10	1.57	0.53	0.0032	3.84	4.68
BAI COV 10	16.36	5.13	0.0014	2.33	4.81
RD total area slope 10	47	26.62	0.0774	1.14	1.56
RD total area COV 50	3.71	2.2	0.0918	0.76	1.2
BA abco slope 5	-14.45	8.16	0.0768	-1.00	1.32

Note: VIF is the variance inflation factor.

Discussion

Differences between live and dead

Overall our results suggest that large sugar pine could be more susceptible to mortality when growth in individual trees had a declining growth trend, experienced a higher occurrence of abrupt declines, and had a lower year-to-year variability. The greatest difference was found in the 10 year slope of BAI, suggesting that large and dead sugar pine would more likely have a declining growth trend as opposed to lower relative growth. This result is consistent with other research that also found decreasing growth trends to be associated with the probability of mortality in conifers (Bigler and Bugmann 2003; Das et al. 2007; Kane and Kolb 2014). We did find dead sugar pine to have a higher occurrence of abrupt growth declines over 50 years, which is in line with Pederson (1998), who suggested that past events leading to a sudden decreased growth may inform mortality models better than just slower average growth. Live sugar pine also had higher variability 10 years before mortality, signifying greater sensitivity to changes in the environment, and this finding is also consistent with previous studies (Ogle et al. 2000; Kane and Kolb 2014). Specifically, Ogle et al. (2000) found lower sensitivity in older trees to be associated with a higher probability of mortality. Individual trees that have higher variability in growth may be more responsive to environmental changes and take advantage of more favorable conditions.

The result that live sugar pine had more resin duct total area than dead sugar pine is consistent with past research. Hood et al. (2015) found that live ponderosa pine had

significantly higher total area compared with dead ponderosa pine. More resin duct area implies a larger reservoir of resin, and large sugar pine with more resin duct total area may be more successful at pitching out bark beetles by simply having more resin available. Although there was no statistical difference, year-to-year variability in resin duct total area was higher in live sugar pine. Based on the top mortality model lower variability in resin duct total area could be associated with a higher likelihood of large sugar pine mortality. Over the 50 years analyzed, resin duct production was essentially equal between dead and live sugar pine (3.63 ducts y^{-1} and 3.41 ducts y^{-1} , respectively). This was surprising considering Kane and Kolb (2010) found more resin ducts in surviving ponderosa pine and Ferrenberg et al. (2014) found more resin ducts in bark beetle resistant lodgepole pine and limber pine. There was also no statistical difference in resin duct size; however differences in resin duct size may still have biological importance. Applying Poiseuille's law to resin flow, where small increases in resin duct size should increase resin flow by the fourth power (Schopmeyer et al. 1954), highlights the physiological importance of resin duct size. Large sugar pine with slightly smaller resin ducts could be less successful in resisting bark beetle attack because of higher resistance in flow, even when resin duct production is relatively similar to live trees. Numerous studies have shown that pines with higher resin flow also are less prone to bark beetle attack (Nebeker et al. 1992; Strom et al. 2002; Perrakis et al. 2010).

There was no noticeable difference in total competition between live and dead sugar pine, which was surprising considering other studies have found competition to be significant contributor to tree mortality. For example, in another old-growth forest of the

Sierra Nevada, dead trees typically had more competitors (Das et al. 2011). Competition was also the primary factor driving changes in tree mortality in western Canada (Zhang et al. 2015). Even more surprising was that our results found significantly higher basal area of intraspecific competition around live sugar pine, when Das et al. (2008) found an increased mortality risk for sugar pine that had more competition with other pines. However, competition may not dominate mortality processes in older stands, where there is a high amount of variability in the role of competition (Franklin and van Pelt 2004, Das et al. 2008). Sampled large sugar pine had dominant or codominant crowns, and competition from smaller trees likely had minimal impacts on limiting light resources. At our site sugar pine may be favored under specific microsite conditions, leading to clusters of sugar pine stands that limit ingrowth from more shade tolerant species that may drive changes in competition when fire is excluded. Another possible explanation could be that clusters of sugar pine share resources through mycorrhizae or root grafting could overcome threats from biotic agents. Das et al. (2008) found a similar facilitative effect for white fir and red fir where surviving trees tended to have a higher density of the same species. Finally, we recognize that our paired design may have controlled for differences in competition because paired trees were in close proximity and presumably in similar stand conditions. Therefore, the full range of competition was not accounted for, and there was a lack of sufficient variation between live and dead sugar pine.

Large sugar pine mortality models

To our knowledge this is the first study that compared the relative importance of growth, defense, and competition on pine mortality. Our results suggest that including measures of growth, defense, and competition improved the performance of large sugar pine mortality models at our site. Moreover, combining two categories of growth, defense, or competition improved mortality models over models that included only one category (Table 4). This result was consistent with the top performing models from Ferrenberg et al. (2014) that included both growth and defense. Measures of competition improved mortality models from a base model that included recent growth (Das et al. 2008).

When comparing the relative importance of growth, defense, and competition, we found growth only models to have a lower AICc than defense only and competition only models. Our results suggest that resin duct properties did not better estimate the probability of mortality than growth as was found in Kane and Kolb (2010). Unlike previous research (Kane and Kolb 2010; Hood et al. 2015), pine trees in our study site did not have evidence of a recent high mortality event and large sugar pine mortality remained low (<10 %). We suggest that resin duct defenses can improve pine resistance to bark beetle attack even when bark beetle related mortality is low, but other contributing factors to tree mortality (e.g. climate and competition) have a stronger influence.

Our study found shorter and more recent time windows for growth, resin duct total area, and competition were more important than longer time windows and past

measurements. Other studies have found both long-term and short-term growth to be informative (Bigler and Bugmann 2003; Kane and Kolb 2014), while Das et al. (2007) found long-term trends (40 years) to be more informative for sugar pine specifically. However, the 50 year coefficient of variation in resin duct total area was included in four of the top five mortality models, suggesting that resin duct total area in live sugar pine maintained a higher sensitivity to changes in the environment over a longer time period. 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. It is also possible that past events causing changes in growth, defense, and competition were not accounted for in the 50 years analyzed in this study, and future research could extend the time period analyzed.

Future implications

Although we did not examine the effects of climate on large sugar pine mortality, future climate conditions in California may also be important in large sugar pine mortality. Conifer growth in high elevation forests of the Sierra Nevada have shown multidecadal responses to climate (Millar et al. 2004; Bunn et al. 2005), and changes in pine resin duct defense are also influenced by climate (Hood et al. 2015). Furthermore, dense and overgrown forests resulting from fire suppression are widespread in the Sierra Nevada, and higher mortality during drought events has been found in denser stands (Guarín and Taylor 2005). During extreme drought events, large sugar pine with more competition may be more susceptible to mortality, and the relative importance of

competition on sugar pine mortality could be higher. It should be noted that most of our sampled sugar pine died prior to the most recent drought event in California. Finally, climate change may have compounding negative effects on large sugar pine mortality by increasing bark beetle activity and decreasing resin duct defenses. Warmer winter temperatures associated with climate change have been linked to increases in bark beetle activity (Raffa et al. 2008), and increasing climatic water deficit in the Sierra Nevada has been linked to decreasing resin duct size and total area (see Chapter 1).

Climate projections for California predict warmer temperatures and a higher variability in precipitation, suggesting that the Sierra Nevada could see a higher occurrence of temperature driven drought and a higher severity of drought (Dettinger et al. 2004). Large tree mortality is most impacted by droughts in forests worldwide (Bennett et al. 2015), and managers across the region may want to consider restoration treatments to improve resistance to drought if maintaining large sugar pine is an objective. Research has shown higher growth sensitivity to climate under lower levels of competition (Sánchez-Salguero et al. 2015), and our results suggest higher sensitivity of growth and defense measures were associated with sugar pine survival. Thinning treatments designed to reduce tree density and overall competition, may allow remnant large sugar pine to increase their vigor during favorable climate conditions. Similar treatments may also improve resin duct defense and reduce large sugar pine susceptibility to mortality from bark beetles. For example, Hood et al. (2015) found that resin duct defenses were higher following low intensity fire, and a combination of forest thinning and prescribed fire may be necessary to conserve large sugar pine in the future.

Finally, our results showed that a higher rate of decreasing white fir competition (i.e. mortality) was associated with a reduced probability of mortality, and live sugar pine tended to occur in clusters of large sugar pine with a higher basal area of intraspecific competition. Therefore, both thinning and prescribed fire treatments could target white fir, prioritizing stands containing a high proportion of white fir.

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CONCLUSION

This study has many important findings that have implications for large sugar pine vigor and mortality in the central Sierra Nevada. First, competition appears to have a greater effect on growth and defense than climate, but both factors are informative. There are contrasting impacts in how climate change could affect large sugar pine vigor and mortality in the future. Individual trees could increase vigor in terms of growth, especially if large sugar pine growth continues to be best associated with increasing January temperature. However, rising winter temperatures could also continue to increase climatic water deficit, which may lead to a decrease in both resin duct total area and resin duct size. There are also contrasting impacts of competition on resin duct defenses. In stands with higher total competition resin ducts may be smaller because of fewer available resources; however, competitive stress could induce higher resin duct production, increasing total area. As a consequence, large sugar pine might have a larger reservoir of resin to pitch out invading pests, but less efficiency when transporting resin to the site of attack.

Growth, defense, and competition were all associated with large sugar pine mortality. Declining growth 10 years before tree death had the largest effect on increasing mortality risk. Surprisingly, large sugar pine at the study site tended to have higher intraspecific competition, and grew significantly higher than dead sugar pine from 50 to 10 years before tree death. Climate change could increase mortality risk for large sugar pine. Warmer winter temperatures could lead to increased bark beetle

activity, but also increase climatic water deficit by altering evapotranspiration, leading to fewer resin duct defenses.

Forest managers interested in perpetuating large sugar pine may consider thinning and prescribed fire treatments to improve vigor and reduce mortality risk. However, treatments with the goal of reducing total competition may have the unintended consequence of decreasing resin duct total area, which is associated with a higher probability of mortality. The composition of competition matters, and thinning treatments may target white fir competition because live sugar pine is associated with decreasing white fir competition and higher intraspecific competition. Finally, reduced competition could increase the sensitivity (i.e. annual variability) of growth and defense to changes in climate. Higher variability in growth and resin duct total area is associated with a lower probability of mortality in large sugar pine.

Even though this study provides a better understanding on the relationships between large sugar pine vigor, mortality, climate and competition, more information is needed. Future research could address the mechanisms behind the clusters of large sugar pine that were often associated with lower growth, but also lower mortality. Furthermore, environmental change in recent decades could also alter climate and large sugar pine vigor relationships, and understanding how these relationships change over time could help guide adaptable management plans. Finally, the relationship between resin duct defenses and competition is complicated and more information is need on the mechanisms that induce resin duct production and limit resin duct size.

APPENDIX A

APPENDIX A. Species and site- specific equations to estimate diameter at breast height (DBH) from basal diameter (BD; bark thickness (BT) from DBH; and last year of growth in dead trees from decay class and DBH. All equations were constructed using linear regression.

Species	Diameter at breast height (cm)			Bark thickness (cm)		
	n	Equation	r ²	n	Equation	r ²
White fir (<i>Abies concolor</i>)	1622	DBH = 0.8224*(BD) - 0.5528	0.99	365	BT = 0.067113*(DBH) + 0.102079	0.84
Incense cedar (<i>Calocedrus decurrens</i>)	731	DBH = 0.8306*(BD) - 1.9841	0.99	221	BT = 0.092977*(DBH) + 0.057822	0.85
Sugar pine (<i>Pinus lambertiana</i>)	387	DBH = 0.8779*(BD) - 2.9493	0.99	189	BT = 0.059215*(DBH) + 0.658114	0.78
Jeffrey pine (<i>Pinus jeffreyi</i>)	41	DBH = 0.8470*(BD) - 2.1238	0.98	51	BT = 0.070095*(DBH) + 0.404598	0.82
Ponperosa pine (<i>Pinus ponderosa</i>)	30	DBH = 0.8463*(BD) - 2.7109	0.98	40	BT = 0.061901*(DBH) + 0.833514	0.78
Last year of growth (year)						
Species	n	Equation			r ²	
White fir (<i>Abies concolor</i>)	19	Year = 2013.37395-3.01157*(decay class) + 0.05148*(DBH)			0.67	
Incense cedar (<i>Calocedrus drecurrens</i>)	20	Year = 2016.96708-5.24412*(decay class) + 0.09327*(DBH)			0.62	
Sugar pine (<i>Pinus lambertiana</i>)	13	Year = 2012.73560-3.76571*(decay class) + 0.02657*(DBH)			0.76	