COMPETITION, CLIMATE, AND DROUGHT EFFECTS ON TREE GROWTH IN AN ENCROACHED OAK WOODLAND IN NORTHERN CALIFORNIA

By

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ABSTRACT

COMPETITION, CLIMATE, AND DROUGHT EFFECTS ON TREE GROWTH IN AN ENCROACHED OAK WOODLAND IN NORTHERN CALIFORNIA

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Oregon white oak (*Quercus garryana* Douglas ex Hook.) is experiencing increasing competition from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) across its range at the same time as climate models are predicting increasing climate variability, including drought. Management recommendations that consider competition dynamics between these species under a changing climate are therefore needed for oak woodlands, but we do not currently understand the combined effects of competition, climate, and drought in this ecosystem. This research examines radial tree growth and drought response in Oregon white oak and Douglas-fir in an encroached oak woodland near Kneeland, California. Stem maps of local crowding competition were created for 104 Oregon white oak and 104 Douglas-fir trees that were sampled for growth across Douglas-fir encroachment levels. Linear mixed effects models were used to evaluate the effects of DBH, Douglas-fir crowding, oak crowding, and climate on tree growth (2002-2016) and drought response (2013-2015). Oregon white oak growth had positive relationships with November-January precipitation, July-August precipitation, April-June mean maximum temperature, and September maximum temperature; and negative relationships with oak crowding, Douglas-fir crowding, and summer maximum temperature. Douglas-fir growth had a positive relationship with May-June precipitation and negative relationships with Douglas-fir crowding and June-July mean maximum temperature. Oregon white oak growth was more resistant to prolonged drought than Douglas-fir. However, oak resistance to drought was also negatively related to Douglas-fir crowding and positively related to oak crowding. Oregon white oak may be better suited to a future climate than Douglas-fir, but Douglas-fir encroachment will continue to degrade this ecosystem and threaten the ability of Oregon white oak to resist future drought. Prevention and management of Douglas-fir encroachment in oak woodlands is therefore encouraged to preserve ecosystem function under climate change.

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INTRODUCTION

An improved understanding of how competition, climate, and drought affect tree vigor and stand dynamics in forest ecosystems is critically needed to inform management of today's forest ecosystems for the ecological and climate conditions of tomorrow. In California, increased climate variability is projected through the 21st Century, including increases in both drought and extreme hydrological events (Swain et al. 2018). Patterns of precipitation and temperature vary seasonally, and although these seasonal patterns are not projected to shift in California, an amplification of the existing Mediterranean precipitation pattern is expected (Swain et al. 2018). Tree species also vary in their seasonality of water use, growth, and repair, so changes in precipitation will not affect all species equally (Anderegg et al. 2013). In addition, how climate change affects individual species may depend on fine-scale competition dynamics within forest ecosystems (Gómez-Aparicio et al. 2011). Therefore, it is critical to piece together the ecohydrological context in which meteorological drought translates into tree stress and mortality at the species level, and thus affects ecosystem change (Anderegg et al. 2013). This study contributes to that effort and provides guidance for forest managers by investigating tree-growth response in Oregon white oak (*Quercus garryana* Douglas ex Hook.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) related to competition, climate, and drought in an encroached oak woodland in northwest California.

In the Pacific West, oak woodlands are highly-valued habitats and important for many species, at least in part because of abundant light conditions beneath oakdominated canopies, which support a rich and diverse understory community (Thysell and Carey 2001; Devine et al. 2007; Livingston et al. 2016). These ecosystems, which were once burned and tended by Native Americans, require frequent fire, but fire occurrence has declined dramatically due to cultural genocide and the adoption of fire suppression policy. In the absence of disturbance, Oregon white oak woodlands are vulnerable to encroachment by shade-tolerant conifer trees like Douglas-fir, which can grow quickly through oak canopies (Hunter and Barbour 2001), which is occurring throughout much of the species' range (Thysell and Carey 2001; Cocking et al. 2015). In northwestern California, Douglas-fir establishment in oak woodlands has especially accelerated since the 1970s (Schriver et al. 2018). Oregon white oak is shade-intolerant, and Douglas-fir competition dramatically reduces the availability of photosynthetically active radiation (light) – according to one study by about 87% (Devine and Harrington 2006). Allocation of resources to diameter growth is a low priority in trees, which makes it a good indicator of tree stress, whether caused by competition, climate, or some other factor (Oliver and Larson 1996). As such, increasing competition from late-establishing Douglas-fir is associated with reduced radial growth in Oregon white oak (Gould et al. 2011; Devine and Harrington 2013; Schriver 2015). Unabated, reduced growth from Douglas-fir encroachment leads to oak mortality, and eventually, to complete ecosystem change (Hunter and Barbour 2001; Gould et al. 2011; Schriver et al. 2018).

At the same time as oak woodland ecosystems are converting to closed conifer forest mainly due to an interrupted fire regime, climate change is increasing the likelihood of extreme drought conditions throughout California (Diffenbaugh et al. 2015;

Williams et al. 2015). Drought may induce further stress-related growth declines in forest trees and can also trigger mortality, especially when combined with increased competition (Pedersen 1998; Bigler et al. 2007; Allen et al. 2010, 2015; Bottero et al. 2017; Young et al. 2017; Lalemand 2018; Vernon et al. 2018). Conditions during the prolonged moderate to severe drought that occurred in northwestern California from 2013-2015 (National Drought Mitigation Center et al. 2017) were influenced by anthropogenic warming and may be exemplary of future severe drought conditions (Williams et al. 2015; Swain et al. 2016). Therefore, analysis of tree growth before and during this event provides a unique opportunity to examine the effects of competition, climate, and drought to help inform future management of this ecosystem under climate change.

Forest ecologists and managers have long recognized the effect of competition from other trees on tree growth and stand development (Reineke 1933; Tilman 1982; Oliver and Larson 1996). While the concepts of niche partitioning and succession dynamics are understood to play important roles in forest ecosystems, species-specific competitive effects on tree-growth from differing competitor species are often ignored in ecological research and forest growth models (e.g. Keyser 2008; Sánchez-Salguero et al. 2015; Zhang et al. 2015; Carnwath and Nelson 2016; Young et al. 2017; Lalemand 2018; Vernon et al. 2018), perhaps due to the vast complexity of many forest ecosystems. Researchers who have investigated species-specific competition have shown that these relationships are unique for each species pair, and provide a more detailed understanding of competition dynamics within forest ecosystems (Canham et al. 2004; Coates et al.

2009; Boivin et al. 2010; Gómez-Aparicio et al. 2011; Das 2012). The effect of intraspecific competition on tree growth is likely strong due to similar use of resources among members of the same species (Tilman 1982). While intraspecific competition is the greatest competition factor on growth for many species, this is not true for all species (Canham et al. 2004, 2006; Coates et al. 2009; Boivin et al. 2010; Gómez-Aparicio et al. 2011; Das 2012). Given the shade-intolerance of Oregon white oak and well-documented decline of this species as a result of Douglas-fir encroachment (Barnhart et al. 1996; Hunter and Barbour 2001; Thysell and Carey 2001; Cocking et al. 2015; Schriver et al. 2018), Douglas-fir competition may have a greater influence on Oregon white oak growth than intraspecific competition.

Understory microclimate has been found to be moderated by vegetation density, forest management, and even forest composition (Chen et al. 1993, 1999; Devine and Harrington 2007; Devine et al. 2007; Ashcroft and Gollan 2013; Greiser et al. 2018). Competition measures related to forest density and structure may interact with climate to affect tree growth. In particular, Douglas-fir encroachment may result in multiple microsite changes such as increased interception of rainfall, reduced soil water availability, increased shade, decreased air and soil temperatures, and/or reduced evapotranspirational water loss from soil and forest vegetation. Douglas-fir encroachment may also increase competition for soil moisture. For example, seasonal (May-September) microclimate change has been observed after the removal of encroaching Douglas-fir in Oregon white oak woodlands, including increases in soil water content, precipitation throughfall, soil temperature, maximum air temperature, and vapor pressure deficit (Devine and Harrington 2007; Devine et al. 2007).

The seasonality of drought and climate variability may also influence tree stress and forest ecosystem dynamics. Precipitation patterns affect the availability of soil moisture and the timing of plant water use for physiological processes, including growth and tissue repair (Anderegg et al. 2013). Species-specific anatomical and physiological characteristics such as hydraulic-tissue repair mechanisms and hierarchical investments in root structures, stomatal regulation, and hydraulic-tissue are still not fully understood, but known to be important determinants of how trees respond to the timing and magnitude of drought (Hacke et al. 2006; McDowell 2011; Choat et al. 2012). For example, some California oaks have root adaptations and mycorrhizal associations that provide access to deep water within the granite matrix, hydraulically lifting deep water during dry conditions, while also allowing access to shallow, ephemeral soil moisture from rare but occasional rains during the dry Mediterranean summer (Abrams 1990; Allen 2015; Hahm et al. 2018). There is evidence that Douglas-fir also hydraulically lifts water during dry periods (Domec et al. 2004).

Differences in water transport tissue structure, protection, and repair mechanisms may especially relate to growth during and following prolonged summer drought periods, high temperatures, and associated spikes in vapor pressure deficit (McDowell et al. 2008; Allen et al. 2010; Eamus et al. 2013). While both species regulate stomatal conductance in response to water stress, Oregon white oak withstands lower daytime leaf water potentials with less daily loss of relative leaf conductivity and daytime stomatal closure compared to Douglas-fir when measured at the same site (Johnson et al. 2009). Growth in Douglas-fir is affected by water availability and temperature interactions during the growing season (Case and Peterson 2005; Carnwath et al. 2012; Beedlow et al. 2013). Temperature, as a critical driver of vapor pressure deficit (Eamus et al. 2013), affects growth of Douglas-fir more during periods of ample soil water, suggesting that stomatal regulation leads to growth declines in this species during prolonged periods of drought and temperature stress (Beedlow et al. 2013). Additional research shows that Oregon white oak is able to maintain sap flow during dry conditions in spite of increasingly low shoot water potential values (Hahm et al. 2018). This suggests that Oregon white oak photosynthesis and growth may be maintained during dry conditions due to less stomatal regulation and daily loss of conductivity relative to Douglas-fir. However, Oregon white oak and other ring-porous species are vulnerable to xylem embolism with severe decreases in xylem water potential (Hacke et al. 2006; Johnson et al. 2012), which may affect growth.

Species-specific physiological mechanisms of tree stress are still being investigated by other researchers, but radial stem growth in both species is expected to be reduced during drought. Compared to Oregon white oak, it seems likely that Douglas-fir growth may be more impacted by prolonged drought periods and consistently warm temperatures during the growing season due to sustained stomatal closure and daily loss of conductivity (McDowell et al. 2008; McDowell 2011). Oak growth may be more resistant to prolonged drought, but sensitive to extreme vapor pressure deficit associated with summer maximum temperatures during dry conditions (Hacke et al. 2006).

In relation to existing research highlighted above, this study evaluated the following research questions and hypotheses:

1) Controlling for tree size, how do competition and climate affect radial growth in Oregon white oak and Douglas-fir?

I expect Douglas-fir competition is more influential on growth of both Oregon white oak and Douglas-fir than oak competition. I also expect growth in both species to be positively related to precipitation with a negative interaction (less positive effect of precipitation) with Douglas-fir competition in Oregon white oak. I expect growth in Oregon white oak to be negatively related to summer maximum temperatures with a positive interaction (less negative effect of summer maximum temperature) with Douglas-fir competition. In addition, I expect Douglas-fir growth to be negatively related to maximum temperatures throughout the growing season.

2) How do Oregon white oak and Douglas-fir differ in their resistance to drought, and how does competition affect drought resistance?

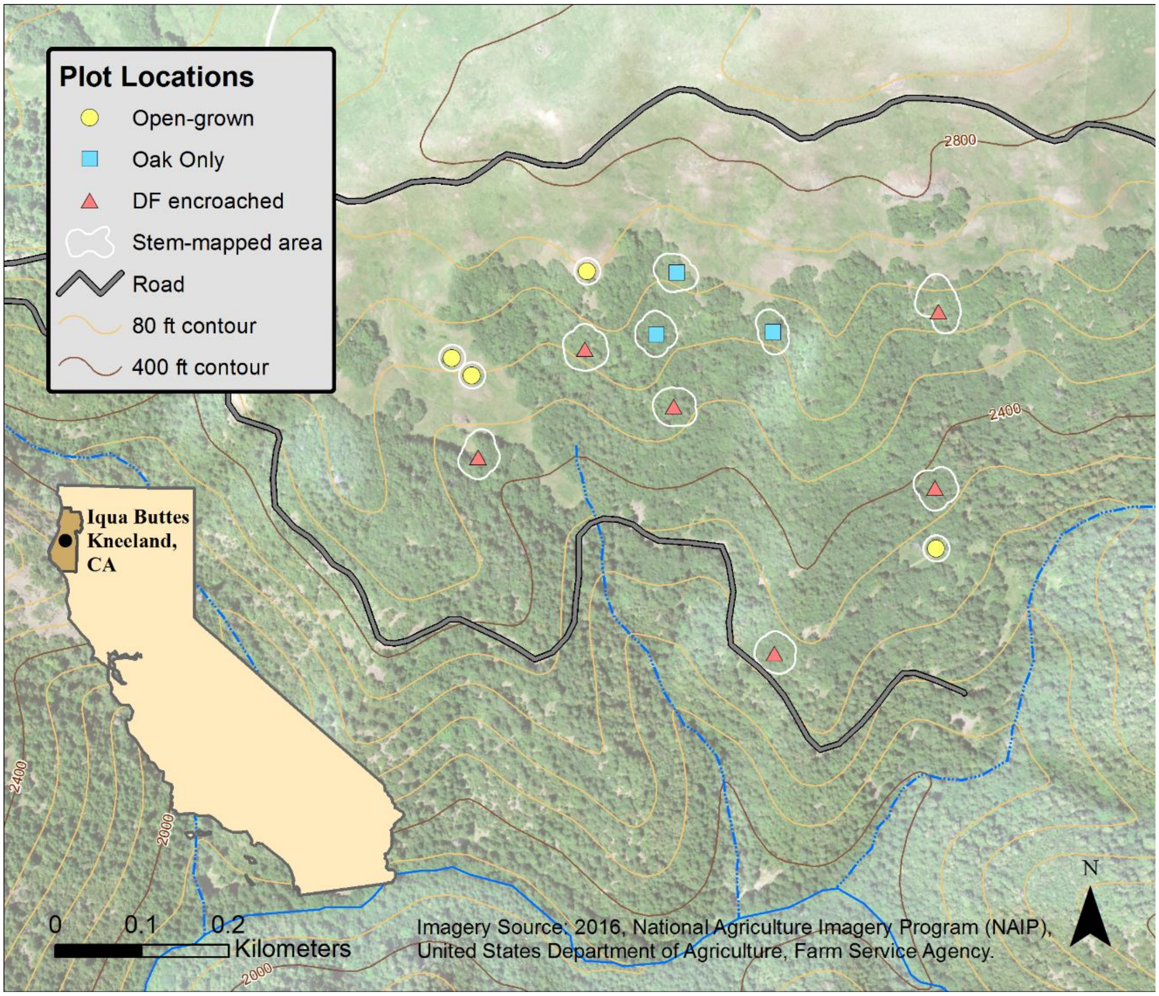
I expect lower drought resistance for Douglas-fir than for Oregon white oak. I also expect drought response in both species to be negatively related to competition.

MATERIALS AND METHODS

Study Area

The study site is located in Humboldt County near Kneeland, California within an Oregon white oak woodland located on private land (Humboldt Redwood Company). The Mediterranean climate has historically average temperatures of 7.0 °C in December and 18.4 °C in July, and annual precipitation of 1743 mm with most falling between October and May (PRISM Climate Group 2017). The area is within the Franciscan Complex area of the Coast Range Province, composed primarily of sedimentary and meta-sedimentary rocks. Soils are fine loamy to loamy skeletal and shallow in some places, as evidenced by occasional nearby rock outcrops (Marshall 2017). Slopes are generally steep, varying from 19-35° across plot locations with a generally southern aspect ranging SE to SW (Table 1). The estimated historic fire return interval within the study area is 6-10 years (LANDFIRE 2017), but no recorded fire has occurred at our site at least since 1900 (California Department of Forestry & Fire Protection 2017).

Previous research and historical photos indicate that Douglas-fir was not abundant on the site until the mid to late 20th century (Schriver 2015). This contrasts with the establishment of Oregon white oak that dates from the early 1800s, with most establishment occurring between 1865 and 1930 (Schriver 2015). California black oak (*Quercus kelloggii* Newberry) is less abundant but also present, with similar establishment dates as white oak. Douglas-fir encroachment is patchy throughout the site, but generally greatest at middle and lower slope positions, with grasslands and pure oak stands most commonly occurring on upper slopes (Figure 1). This suggests an apparent relationship between site quality and slope position, but a recent soil evaluation was not able to establish a relationship between available soil water holding capacity and the degree of Douglas-fir encroachment or slope steepness (Marshall 2017).



Imagery Source: 2016, National Agriculture Imagery Program (NAIP), United States Department of Agriculture, Farm Service Agency.

Figure 1: Plot locations at the sampling site near Kneeland, California.

Study Design

I collected data in nine plots that were randomly selected in 2013 as part of a regional study on oak woodland habitats (Schriver et al. 2018). These nine plots were evenly stratified based on three general forest conditions (3 plots in each; Table 1). ‘Open’ stands were characterized as oak-dominant stands where conifers were not present or limited to the sub-canopy. ‘Transitional’ stands were characterized as oak-dominant stands with Douglas-fir in an intermediate or co-dominant canopy position. ‘Closed’ stands were characterized as oak stands where Douglas-fir occupied the dominant canopy position or was emergent in the canopy throughout the stand (Schriver et al. 2018). I resampled and increased the size of these plots to build upon the existing 2013 dataset, and adjusted one plot center uphill in order to avoid a riparian zone that comprised almost half of the increased plot dimensions. In addition to trees within the established plots, four ‘open-grown’ Oregon white oak trees were opportunistically sampled outside of the nine plots to account for Oregon white oak growth in conditions absent of competition from other trees, a condition that was present at the site but not within the nine randomly-located forested plots (Table 1).

Table 1. Stand type, encroachment group, Douglas-fir (DF) crowding (Hegyi), aspect (°), slope (°), and elevation (m) mean and range values by plot. Stand type was defined by Schriver et al. 2018.

Plot No	Stand Type	Encroachment Group	DF Crowding (Hegyi)	Aspect (°)	Slope (°)	Elevation (m)
1	Closed	DF encroached	7.58 (0.92 - 23.00)	222 (204-238)	35 (20-43)	790 (771-809)
2	Open	Oak only	0.27 (0.00 - 0.86)	134 (105-181)	21 (10-38)	790 (780-799)
3	Open	Oak only	0.10 (0.00 - 0.32)	210 (156-245)	21 (10-32)	808 (797-817)
4	Open	Oak only	0.14 (0.00 - 0.28)	185 (170-209)	24 (19-31)	786 (773-798)
5	Transitional	DF encroached	4.10 (0.86 - 8.06)	185 (145-209)	33 (17-40)	797 (774-817)
6	Transitional	DF encroached	2.07 (0.40 - 5.76)	147 (135-182)	29 (18-37)	722 (709-735)
7	Transitional	DF encroached	5.78 (1.34 - 14.70)	221 (203-248)	25 (15-31)	694 (682-704)
8	Closed	DF encroached	5.47 (2.36 - 12.10)	115 (94-155)	24 (12-32)	766 (755-778)
9	Closed	DF encroached	5.45 (1.64 - 15.70)	131 (83-236)	22 (6-44)	741 (730-750)
OG-1	Open-grown	Oak only	0.00	136 (132-141)	21 (18-23)	697 (691-702)
OG-2	Open-grown	Oak only	0.00	183 (177-187)	23 (23-24)	780 (774-785)
OG-3	Open-grown	Oak only	0.00	188 (186-190)	23 (21-24)	787 (781-793)
OG-4	Open-grown	Oak only	0.00	185 (130-223)	19 (10-29)	830 (824-834)

Field Methods

Fieldwork was conducted in fall 2017 and spring 2018, and included coring all Oregon white oak and Douglas-fir trees (any stem differentiated below breast height, 1.37 m) within 10 m of each plot center. Trees were cored with a 4.3 or 5.15 mm borer parallel to the slope at an average height of 0.93 m (SD = 18.22). All trees greater than 10 cm diameter at breast height (DBH) for Douglas-fir and greater than 5 cm DBH for oaks that were within 15 m of each cored tree were mapped and inventoried for species, DBH, crown class, damage, multi-stem status, and if applicable, coring height and diameter at coring height. To increase sample size, additional trees were opportunistically cored within 15 m of plot center if the required stem map expansion work was minimal. A total of 108 Douglas-fir and 120 Oregon white oak subject trees were cored.

Lab Methods

Tree-growth response

Tree cores were mounted and incrementally sanded with a maximum of 600 grit sand paper in order to improve visibility of tree-ring boundaries. Mounted tree cores were digitally scanned at 1200 dpi for Douglas-fir trees and 2400 dpi for Oregon white oak trees and measured using WinDENDRO software (Regent Instruments 2014). A dissecting microscope was used to identify and confirm visibility of each ring boundary, especially while measuring the most challenging cores. Visual cross-dating methods were first used, and all measured cores were subsequently statistically cross-dated using Program COFECHA (Holmes, 1983). We successfully cross-dated tree cores from 104 Oregon white oak trees and 104 Douglas-fir trees. For most trees only one sample was available for each subject tree. The only exception was for 28 small diameter Douglas-fir where the borer penetrated both sides of the tree and the average was taken for annual growth across the two sides of the tree. In general, Douglas-fir cores were complete from pith (or near pith) to bark, with an average series length of 37 years (range 11-79). Oregon white oak cores were not often complete from pith to bark. The average Oregon white oak series length is 86 years (range 28-154), while the average estimated age is 123 years (range 67-194; Schriver 2015).

Each tree series was detrended by calculating a basal area increment (BAI) using the package *dplR* in R (Bunn et al. 2018; R Core Team 2019). Bark thickness was directly measured on mounted cores for 74 Oregon white oak trees that clearly showed complete inner and outer bark. To estimate bark thickness for trees with incomplete bark samples, bark measurement data were used to derive a non-linear model using the form:

$$Bark\ thickness\ = a \times \sqrt{DCH^{b}}$$

where bark was measured in millimeters, DCH was diameter at coring height in centimeters, and a and b were coefficients derived from the data, using the nls function in R (Zeibig-Kichas et al. 2016; R Core Team 2019). The selected coefficient values for white oak were a = 2.2721 and b = 0.6757, resulting in a standard error of the regression of 2.56 mm for modeled bark measurements that have a mean of 7.38 mm.

For Douglas-fir, a published model was used to estimate Douglas-fir bark thickness from DBH (Zeibig-Kichas et al. 2016). This model is:

$$DF\ Bark\ thickness = 0.785 \times \sqrt{DCH}$$

where bark thickness was measured in millimeters and DCH was diameter at coring height in centimeters. Mean BAI through the analysis period for each species is shown in Appendix C.

Crowding competition

To account for local competition, a total of 1141 competitor trees were mapped within 15 m of all cored trees. Of these, 532 (47%) were Oregon white oak, 500 (44%) were Douglas-fir, 90 (8%) were California black oak, 18 (1.6%) were California bay laurel (*Umbellularia californica* (Hook. & Arn.) Nutt.), and 1 (<0.1%) was tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P.S. Manos, C.H. Cannon, & S.H. Oh). Competitor trees were grouped into two categories, Douglas-fir competitors, and other, non-Douglas-fir competitors. This later group was comprised of only hardwood species with 97% oak species of which 83% were Oregon white oak. Therefore, this group is referred to as “oak” competitors, and can be interpreted as mostly containing conspecific Oregon white oak.

To estimate local competition (variable names ‘Douglas-fir crowding’ and ‘oak crowding’), the Hegyi index was calculated using the equation:

$$Hegyi_t = \sum_{i=1}^{n} \frac{DBH_i}{DBH_t} \times \frac{1}{dist_i}$$

where $Hegyi_t$ represents the competitive strain on the cored subject tree t, DBH_t is the DBH of the subject tree, DBH_i is the DBH of each competitor tree i, and $dist_i$ is the distance between them, summed for all competitor trees within a chosen radius length (Hegyi 1974). The Hegyi index was calculated for each tree in two different ways: Only Douglas-fir competitors and only oak competitors. Radii lengths were selected for each subject tree species – competitor group pair by comparing Pearson correlation coefficients of the 15-year (2002-2016) tree-level mean of basal area increment and separate Hegyi indices of Douglas-fir competitors and oak competitors at radii lengths varying from 1-15 m (Sánchez-Salguero et al. 2015). For all subject tree species – competitor group pairs, a 15 m radius resulted in the strongest correlations.

Climate data

For each plot location, monthly climate data were extracted from the Basin Characterization Model, a 270 m downscaled climate model dataset for California (Flint and Flint 2014). These data include monthly precipitation (PPT, in mm), minimum temperature (TMN, in °C), maximum temperature (TMX, in °C), and climatic water deficit (CWD, in mm). The model and data utilizes a watershed approach to account for local topographic and geologic conditions at the 270 m pixel size.

As an exploratory means to identify significant growth and monthly climate relationships, I reviewed correlations that also had a biological basis during the most recent decades just prior to and during my analysis period (1992-2016). For both Oregon white oak and Douglas-fir, I first developed averaged and prewhitened ring-width indices for each species using *dplR* in R to correlate growth with monthly climate data (PPT, TMN, TMX) (for the methods see Bunn et al. 2018). I then used the *treeclim* program in R to create bootstrapped response correlations and moving monthly correlations, with a window size of 20 years (minimum window length), an offset of 5 years, and $\alpha = 0.05$ (Zang and Biondi 2015; R Core Team 2019).

Based on the correlation analysis, the following variables were selected for further analysis for the Oregon white oak series: November-January PPT, September TMX, late April-June TMX , and July-August PPT. Variables selected for further analysis for the Douglas-fir series include: May-June TMX, and June-July PPT. In addition, summer TMX (occurring usually in July, August, or less commonly September), which could not be used in *treeclim*, was also selected for analysis for Oregon white oak trees (Question 1 hypothesis). To account for lagged climate effects, mean annual CWD for the previous year (November-October) was also selected for further analyses in both species. November through October was selected because of documentation of active sapflow during the month of October in Oregon white oak at a nearby site (Hahm et al. 2018), cambial activity in mid-elevation Douglas-fir through October (Beedlow et al. 2013), personal observation of green (slowly turning) Oregon white oak foliage at the site during October (2017), and monthly CWD estimates recover annually by the end of October. Mean CWD for the current year was not included because it correlated with significant climate variables ($r > 0.6$) and caused instability in some parameter estimates. Climate variability through the analysis period is shown in Appendix B.

Drought response

The study site experienced prolonged and severe drought from 2013-2015 that followed a relatively drought-free period from 2010-2012 (Figure 2; National Drought Mitigation Center 2017). Therefore, drought resistance for each subject tree was calculated using the formula:

$$drought\ resistance = \frac{radial\ growth\ during\ drought}{radial\ growth\ prior\ to\ drought}$$

where radial growth during drought (2013-2015) and prior to drought (2010-2012) was measured in basal area increment (Lloret et al. 2011). This value was calculated for each drought year, and for the entire drought period by averaging basal area increment from 2013 to 2015. In all cases, mean basal area increment for years 2010-2012 was used to indicate radial growth prior to drought.

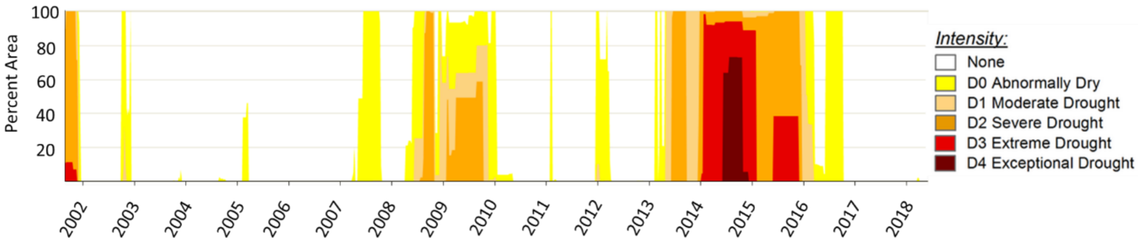


Figure 2. Drought intensity and percent area impacted in Humboldt County, California 2000-2018 (x-axis ticks denote start of calendar year). Severe to exception drought occurred in much of Humboldt County 2013-2015 (National Drought Mitigation Center et al. 2017).

Statistical Methods

I used linear mixed effect models with the package *nlme* in R to evaluate both research questions (Pinheiro et al. 2017; R Core Team 2019). For all models, numeric predictor variables were standardized by subtracting the mean and dividing by two standard deviations to aid in interpretation and comparison of model coefficients (Gelman 2008). Full (all variables included) and selected "best" models were evaluated for homogeneity of variance by viewing plots of residual versus fitted values and for normality by viewing quantile-quantile plots. Multicollinearity was checked using variance inflation factors with a threshold of 3. Best models have variance inflation factors of less than 2.

To evaluate how climate and competition interact as predictors of growth (BAI) in years 2002-2016 (Question 1), I used linear mixed effects models for log-transformed Oregon white oak and Douglas-fir BAI, which included *treeclim*-identified climate variables, Douglas-fir crowding, oak crowding, and DBH as fixed effects. Plot and tree were included as random effects to account for correlation at the plot and subject tree level. To account for temporal autocorrelation, autocorrelations of orders 1-4 were compared using likelihood ratio tests (Pinheiro and Bates 2000). A second-order autocorrelation structure by year was used for Oregon white oak, and a first-order autocorrelation structure by year was used for Douglas-fir because those were the simplest autocorrelation structures for each species that improved Akaike Information Criterion (AIC) by more than 10 over a less complex structure. Due to model complexity (many possible fixed effect combinations), I used a backwards model selection process, starting with a full model that includes all climate and competition terms for each species, and then removed non-significant ($\alpha = 0.05$) terms while checking for AIC improvement. For Oregon white oak subject trees, each important climate variable was then evaluated for interaction with Douglas-fir crowding (encroachment), while also accounting for the other climate and competition effects within each model. Significant interaction terms were retained and AIC comparison was used to select the best climate × competition model (Burnham et al. 2002).

For evaluation of drought resistance (Question 2), two-way analyses of variance (ANOVA) on linear mixed effects models were used to compare drought response for each species, Oregon white oak and Douglas-fir, during each drought year (with random effects of plot and tree) and for the mean drought period (with random effect of plot). An interaction term was evaluated for species and drought year, and differences between groups were identified using Tukey's multiple comparisons with package *multcomp* in R (Hothorn et al. 2019; R Core Team 2019). Additionally, two-way ANOVA were used to compare drought response according to stand-level Douglas-fir encroachment in Oregon white oak trees (encroachment group; Table 1). The "oak only" group included Oregon white oak in unencroached plots and open-grown oak trees and the "DF encroached" group included all plots with any Douglas-fir encroachment (Table 1). Linear mixed effects models, with a random effect of plot, were then used to further evaluate the effect of tree size and competition on drought response. Akaike Information Criterion for small sample sizes (AICc) were used to select the best model with all significant predictor variables ($\alpha = 0.05$) (Burnham et al. 2002).

RESULTS

Question 1: Climate and Competition Effects

The best model for Oregon white oak growth (2002-2016) included positive relationships with September TMX, April-June mean TMX, previous year mean CWD, November-January PPT, July-August PPT and DBH; and negative relationships with summer TMX, oak crowding, Douglas-fir crowding, and the interaction of April-June mean TMX and Douglas-fir crowding (Figure 3). July-August PPT also had a significant interaction with Douglas-fir crowding (Table 2). The best model included the interaction between Douglas-fir crowding and April-June TMX (Table 2, Figure 3). The best model for Douglas-fir growth (2002-2016) included positive relationships with May-June PPT, and DBH; and negative relationships with June-July mean TMX and Douglas-fir crowding (Figure 4).

Table 2. Linear mixed effects models of log-transformed basal area increment (BAI) in Oregon white oak (WO) for years 2002-2016 ($n = 1560$ tree rings). Fixed effects include diameter at breast height (DBH), oak crowding, previous year mean CWD (Nov-Oct), July-Aug PPT, Nov-Jan PPT, Apr-Jul mean TMX, Sept TMX, summer TMX, and a varying interaction (bold lettering) between Douglas-fir (DF) crowding and a climate variable. Dark shading indicates the best model, with no other models within 2 ΔAIC. Table includes all models with all significant predictor variables at $\alpha = 0.05$.

Model Predictors	**AIC**	**ΔAIC**
DBH + oak crowding + previous year mean CWD + Jul-Aug PPT + Nov-Jan PPT + Sept TMX + summer TMX **+ DF crowding * Apr-Jun TMX**	196.25	0.00
DBH + oak crowding + previous year mean CWD + Nov-Jan PPT + Apr-Jun TMX+ Sept TMX + summer TMX + **DF crowding * Jul-Aug PPT + DF crowding * Apr-Jun TMX**	199.64	3.40
DBH + oak crowding + previous year mean CWD + Nov-Jan PPT + Apr-Jun TMX+ Sept TMX + summer TMX + **DF crowding * Jul-Aug PPT**	220.47	24.23
DBH + oak crowding + Douglas-fir crowding + previous year mean CWD + Jul-Aug PPT + Nov-Jan PPT + Apr-Jun TMX + Sept TMX + summer TMX	223.39	27.14

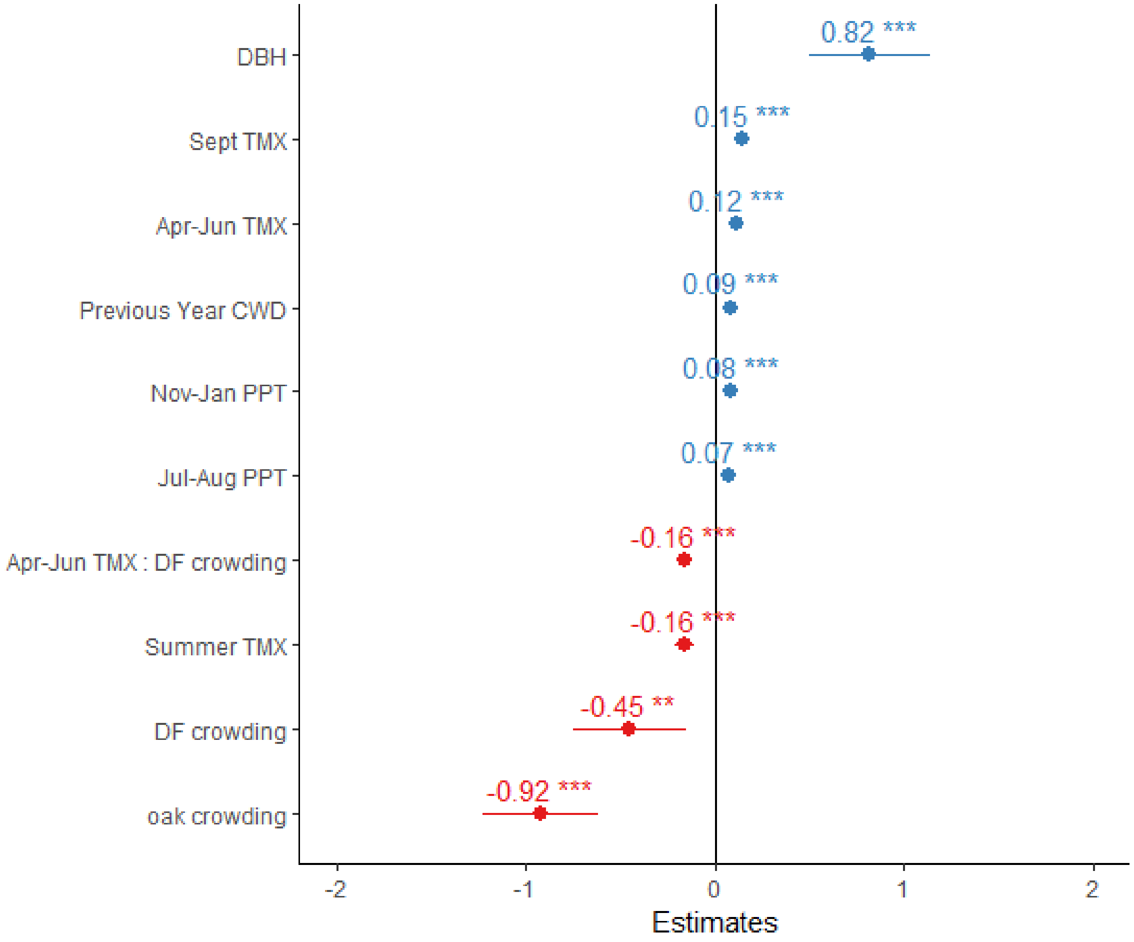


Figure 3. Back-transformed (e^x-1) effect size and 95% confidence intervals of marginal fixed effects on log-transformed radial growth (BAI) in Oregon white oak (WO), years 2002-2016 (*n* = 1560 tree rings). Effect size multiplied by 100 is the percent change in the response variable from a two standard deviation (SD) increase in the predictor variable. DBH (cm) 2 SD = 32.44, Sept TMX (ºC) 2 SD = 2.17, Apr-Jun TMX (ºC) 2 SD = 2.96, previous year CWD (mm) 2 SD = 18.35, Nov-Feb PPT (mm) 2 SD = 603.09, Jul-Aug PPT (mm) 2 SD = 20.43, summer TMX (ºC) 2 SD = 2.13, Douglas-fir (DF) crowding (Hegyi) 2 SD = 5.98, oak crowding (Hegyi) 2 SD = 5.67.

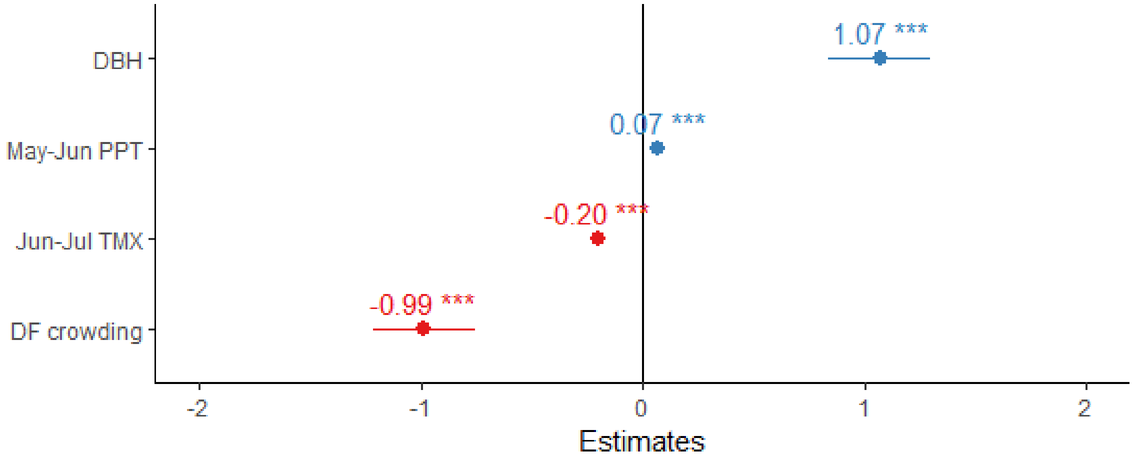


Figure 4. Back-transformed (e^x-1) effect size and 95% confidence intervals of marginal fixed effects on log-transformed radial growth (BAI) in Douglas-fir (DF), years 2002-2016 (*n* = 1529 tree rings). Effect size multiplied by 100 is the percent change in the response variable from a two standard deviation (SD) increase in the predictor variable. DBH (cm) 2 SD = 26.37, May-Jun PPT (mm) 2 SD = 144.87, Jun-Jul TMX (ºC) 2 SD = 3.03, Douglas-fir (DF) crowding (Hegyi) 2 SD = 7.13.

Question 2: Drought Response

There were distinct differences in how Oregon white oak and Douglas-fir responded to the 2013-2015 drought. Mean drought resistance was 24% greater for Oregon white oak than Douglas-fir (WO = 0.93, DF = 0.71, $p < 0.0001$), and some (32%) Oregon white oak had a positive mean growth response to drought (drought resistance > 1). Specifically, Oregon white oak increased drought resistance after 2013 in spite of persistent drought conditions in 2014 and 2015, while Douglas-fir growth consistently declined throughout the entire drought period (Figure 5). Two-way ANOVA on a linear effects model confirmed the presence of an interactive effect of species and drought year ($p < 0.0001$).

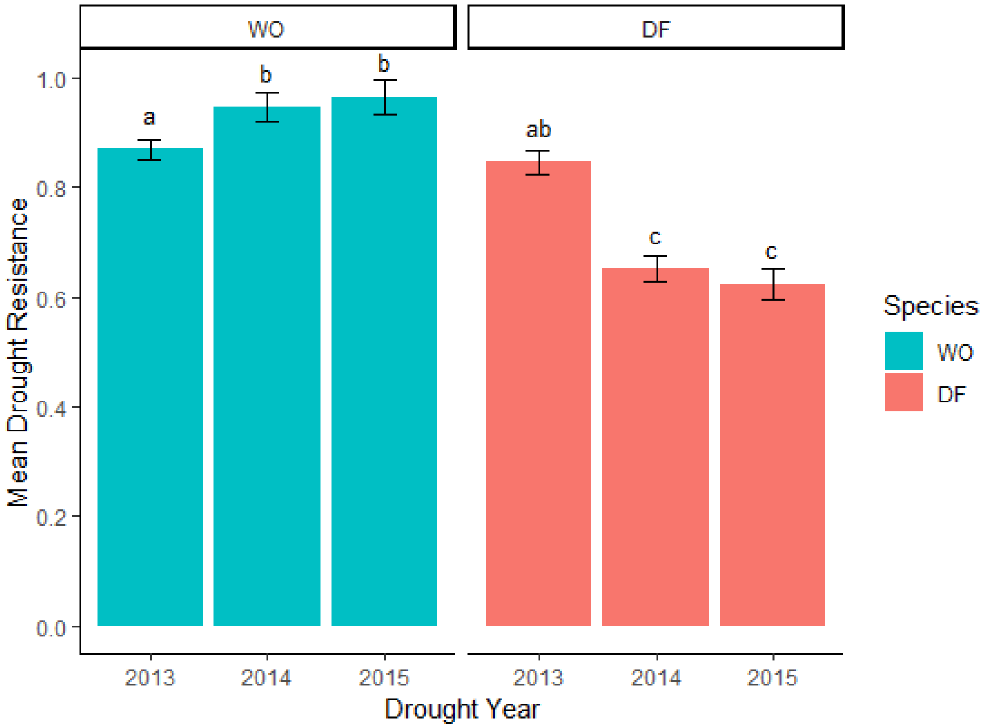


Figure 5. Mean drought resistance in Oregon white oak (WO) and Douglas-fir (DF) by drought year. Letters above standard error bars indicate similar group means according to Tukey's adjustment for multiple comparisons ($\alpha = 0.05$) for two-way ANOVA of a linear mixed effect model with an interaction between species and year, and with random effects plot and tree.

Two-way ANOVA on linear mixed effects models indicated Oregon white oak drought resistance in trees from oak only plots was 15% greater than drought resistance in Douglas-fir encroached plots ($p < 0.001$). Drought resistance of all Oregon white oak in 2014 and 2015 was greater than drought resistance in 2013 (by 8% and 10% respectively, $p = 0.003$ and $p < 0.001$). There was no interactive effect of drought year and stand-level Douglas-fir encroachment group on drought resistance in Oregon white oak trees (Figure 6). Mean drought resistance of Oregon white oak in oak only plots was 1.06 in 2014 and 2015.

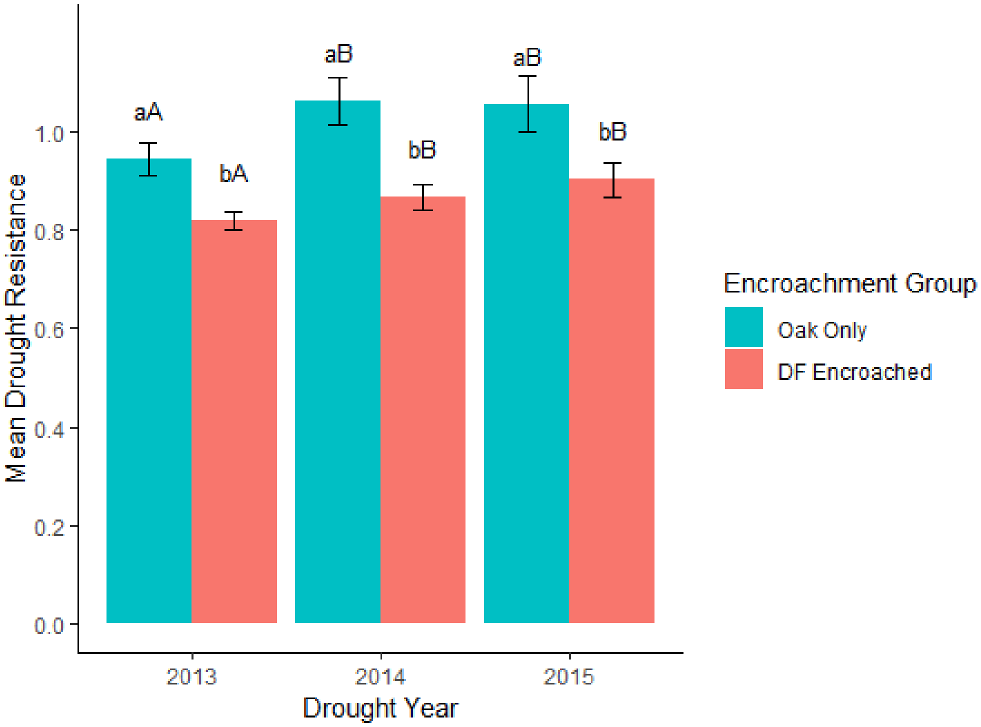


Figure 6. Mean drought resistance in Oregon white oak (WO) grouped by encroachment group and drought year. Letters above standard error bars indicate similar group means according to Tukey's adjustment for multiple comparisons ($\alpha = 0.05$) for two-way ANOVA of a linear mixed effect model and with random effects plot and tree. Lower case letters indicate a difference in means by encroachment group. Capital letters indicate a difference in means in 2013 compared with 2014 and 2015. There is no interaction between encroachment group and drought year.

Mean drought resistance (2013-2015) in Oregon white oak was negatively related to Douglas-fir crowding (effect size -0.15, $p < 0.001$) and positively related to oak crowding (effect size 0.17, $p < 0.001$) (Table 3, Figure 7). Mean drought resistance (2013-2015) in Douglas-fir was negatively related to DBH (effect size 0.16, $p < 0.001$) (Table 4, Figure 8).

Table 3. Linear mixed effects models of mean drought resistance in Oregon white oak (*n* = 104). Fixed effects include diameter at breast height (DBH), oak crowding, and Douglas-fir (DF) crowding. Dark shading indicates the best drought resistance models within 2 ΔAICc. Bold lettering indicates models with all significant predictor variables at $\alpha = 0.05$.

Model Predictors	**df**	**AICc**	**ΔAICc**
oak crowding + DF crowding	**5**	**-8.04**	**0.00**
oak crowding	**4**	**-6.70**	**1.34**
DF crowding	4	-3.71	4.33
DBH + oak crowding + DF crowding	6	-2.26	5.79
DBH + oak crowding	5	-2.08	5.96
DBH	4	-1.82	6.23
DBH + DF crowding	5	-0.04	8.01

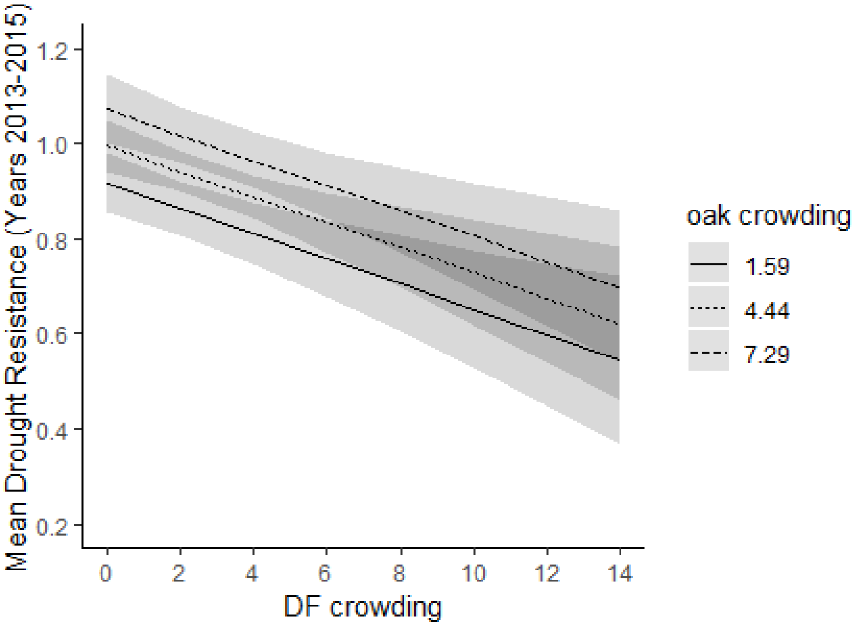


Figure 7. Model predicted mean drought resistance (years 2013-2015) in Oregon white oak trees. Responses at -1 SD, mean, and +1 SD are shown for oak crowding. Model fixed effects for Oregon white oak trees are Douglas-fir (DF) crowding and oak crowding.

Table 4. Linear mixed effects models of mean drought resistance in Douglas-fir (*n* = 104). Fixed effects include diameter at breast height (DBH), oak crowding, and Douglas-fir (DF) crowding. Dark shading indicates the best drought resistance model with no other models within 2 ΔAICc. Bold lettering indicates models with all significant predictor variables at *α* = 0.05.

Model Predictors	**df**	**AICc**	**ΔAICc**
DBH	**4**	**-24.28**	**0.00**
DBH + oak crowding	**5**	**-22.16**	**2.13**
DF crowding	**4**	**-19.30**	**4.99**
DBH + DF crowding	5	-18.19	6.10
DBH + DF crowding + oak crowding	6	-16.93	7.36
oak crowding	4	-13.64	10.64
DF crowding + oak crowding	5	-13.62	10.67

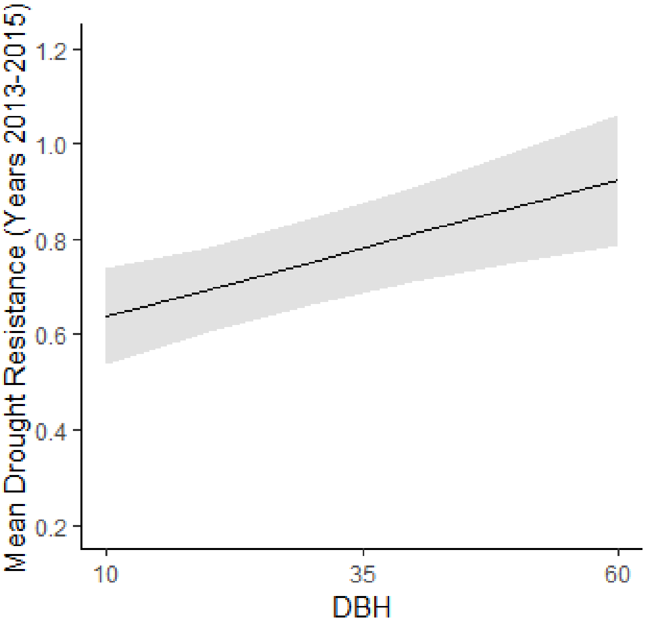


Figure 8. Model predicted mean drought resistance (years 2013-2015) in Douglas-fir trees. Model fixed effects for Douglas-fir trees are DBH only.

DISCUSSION

Climate and Competition

Similar to other climate-competition studies (Gómez-Aparicio et al. 2011; Sánchez-Salguero et al. 2015; Zhang et al. 2015; Carnwath and Nelson 2016), competition had a greater effect on radial growth in both Oregon white oak and Douglas-fir than climate. For both tree species, intraspecific crowding was the most influential factor on radial growth, excluding DBH. This supports my hypothesis for Douglas-fir, but not for Oregon white oak, and indicates that growth in both species was most affected by the presence of conspecific neighbors competing for resources of the same type and/or within the same subsurface strata. Oak crowding was not an important predictor of growth for Douglas-fir trees, which is not surprising given this species' ability to rapidly grow through the canopies of Oregon white oak (Hunter and Barbour 2001).

In addition to competition, I also found several relationships between climate variables and radial growth. Oregon white oak growth benefits most from winter (November-January) and late summer (July-August) precipitation and Douglas-fir growth benefits most from late spring precipitation (May-June). High amounts of winter and early spring precipitation saturate soils and recharge groundwater, while summer precipitation moistens only the very surface of otherwise dry soils (Allen et al. 2010). The association of Oregon white oak growth with winter and summer precipitation may be related to deep roots and arbuscular and ectotrophic mycorrhizal associations that have been documented in other California oaks, which enable them to take advantage of both deep water reserves and rare summer rain events (Abrams 1990; Allen 2015). The association between Douglas-fir growth and late spring precipitation may reflect the effect of some water limitation during the growing season (also see Carnwath et al. 2012; Kelly 2016). This relationship suggests that Douglas fir may be negatively affected by extended dry seasons.

I hypothesized interactive effects on Oregon white oak growth from Douglas-fir crowding and precipitation. I found statically significant interactions between Douglas-fir crowding and July-August precipitation but not with November-January precipitation. Even though the interaction of July-August precipitation and Douglas-fir crowding was not included in the best model, this interaction may reflect increased competition from Douglas-fir for this ephemeral soil moisture or greater interception of precipitation by dense Douglas-fir tree crowns, as previously shown in encroached oak woodland habitats (Devine and Harrington 2007).

As expected, radial growth in Oregon white oak had a negative relationship with summer maximum temperature. This species is able to withstand increasingly low water potential values during summer drought with continued sap flow (Johnson et al. 2009; Kelly 2016; Hahm et al. 2018). It is possible that higher temperatures cause xylem pressure to cross a critical threshold, leading to widespread loss of transport capacity, and thereby reduced radial growth (Hacke et al. 2006; McDowell et al. 2008; Johnson et al. 2012). On the other hand, there is evidence that Oregon white oak also regulates stomatal conductance in accordance with losses in transport capacity (Johnson et al. 2009), so it is also possible that the highest temperatures are affecting growth due to reductions in photosynthesis from stomata closure. Regardless of the exact physiological mechanism, my results indicated that Oregon white oak, while tolerant of dry conditions, is negatively affected by the highest temperatures during summer drought at this site. This is similar to findings in Oregon, where growth in Oregon white oak was negatively related to August maximum temperature over a similar analysis period (Kelly 2016).

Contrary to my hypothesis, I did not find interactive effects from Douglas-fir crowding and summer maximum temperature on Oregon white oak growth. I expected an interaction because increased maximum temperature and vapor pressure deficit have been recorded after the removal of Douglas-fir in Oregon white oak woodlands in Washington state (Devine and Harrington 2007; Devine et al. 2007). The lack of significant interaction could be that temperature change under Douglas-fir does not affect Oregon white oak growth at this site, or may relate to variability in temperature change with Douglas-fir crowding. In addition, the Douglas-fir removed in the aforementioned studies were canopy-dominant trees overtopping oaks while this is not the case for all Douglas-fir competitors at my site. Likewise, a nearly continuous oak overstory in the unencroached ‘oak only’ stands might also moderate summer maximum temperatures and vapor pressure deficit to some level.

In contrast to maximum summer temperatures, late spring (April-June) and early fall (September) maximum temperatures were positively associated with growth in Oregon white oak. I had not hypothesized these relationships. Nevertheless, it is intuitive that warm spring and fall temperatures may serve to elongate the growing season of

Oregon white oak. In addition, the positive relationship between previous year CWD and Oregon white oak radial growth may at least partially reflect a one-year lagged positive effect of April-June mean TMX (highly correlated with CWD; $r > 0.6$).

Warm spring temperatures may be positively associated with growth in Oregon white oak because this is the period in which earlywood vessels enlarge and mature. Warmer temperatures, earlier onset of vessel enlargement, and longer vessel enlargement period have been found to result in larger vessels in other oak species (Kudo et al. 2014; Pérez-de-Lis et al. 2016). Earlywood vessels account for the majority of water conduction and make up much of the actual width of each tree ring (Fonti and García-González 2008). While larger vessels transport water more efficiently, there is a tradeoff between hydraulic efficiency and safety. This tradeoff is advantageously employed by many ring-porous species, though as a result, they may be vulnerable widespread cavitation loss from severe drought (Hacke et al. 2006). My results seem to indicate that at least some of these physiological mechanisms, and tradeoffs, may be affecting growth in Oregon white oak. However, it is unclear that hydraulic efficiency from larger vessels translates into increased radial tree growth under field conditions (Fonti and García-González 2008).

Importantly, I also found a negative interaction of late spring (April-June) maximum temperature and Douglas-fir crowding on Oregon white oak growth. This interaction may reflect reduced maximum temperatures resulting from increased Douglas-fir shading. Although a different forest type, research shows that in boreal forests the ratio of coniferous trees to deciduous trees was associated with an almost 2 ºC reduction in maximum temperature during the month of April only (Greiser et al. 2018).

This effect may have substantial impact at this time of year because oak leaves are not fully formed, and therefore not producing similar microclimate effects in unencroached stands. For example, in both 2017 and 2018 I observed that Oregon white oak broke bud in April, leafed out in May, and only had mature leaves by June.

I hypothesized that Douglas-fir growth would be associated with maximum temperatures throughout the entire growing season, but found only a negative relationship between growth and June-July mean maximum temperature. These findings are similar to results found in Oregon showing a negative relationship of growth and June maximum temperature (Kelly 2016). The negative relationship between Douglas-fir growth and June-July maximum temperatures may be attributed to higher climate-related variability in stomatal regulation during this period compared to later in the summer when stomatal regulation may vary less with temperature due to constant water stress (Beedlow et al. 2013).

Drought Resistance

Both Oregon white oak and Douglas-fir responded negatively to drought in 2013-2015, but the patterns of response are dramatically different. As expected, Douglas-fir responded more strongly than Oregon white oak to prolonged drought. The differences in drought response may be attributed to differences in their physiology (i.e. root structures, seasonal water use, stomatal regulation, and water transport tissue structure). Further, some oaks reduce leaf area in response to drought conditions as part of a conservative strategy that balances low stomatal control and drought-associated decreases in whole tree hydraulic conductance (Limousin et al. 2009). This reduction in leaf area may allow trees to keep a constant, or even increased, leaf-specific hydraulic conductance when submitted to drought stress (Limousin et al. 2009). If present in Oregon white oak, this mechanism could help prevent further damage from continuous drought by limiting tree-level water use and transpiration. In general, oaks have been found to recover quickly from drought events (Anderegg et al. 2015).

Strong legacy effects (reduced growth in years following drought) are associated with lower hydraulic safety margins (Anderegg et al. 2015). Douglas-fir has been found to have a lower hydraulic safety margin than Oregon white oak (Johnson et al. 2009; Kelly 2016). These mechanisms and trends in drought adaptation may be why I found increased resistance of Oregon white oak and decreased resistance of Douglas-fir after the first year of drought. These results also support my hypothesis that Douglas-fir may not be as physiologically adapted to prolonged drought events as Oregon white oak.

As hypothesized, unencroached (‘oak only’) Oregon white oak had greater drought resistance than Douglas-fir encroached Oregon white oak. Further, drought resistance in Oregon white oak was negatively related to Douglas-fir crowding (also see Bottero et al. 2017; Lalemand 2018; Vernon et al. 2018). Trees in high competition environments have reduced crown area (Oliver and Larson 1996). Oregon white oak trees in encroached conditions also invest more in height growth than trees in unencroached conditions (Appendix A; and also see Schriver 2015), in an effort to capture more direct sunlight away from Douglas-fir shading. Reduced crown area in encroached Oregon white oak likely contributed to reduced growth and also may have reduced resistance to drought conditions. This could be related to scarcer resources and prioritization away from structures that aid in drought resistance, such as roots. For example, a decline in hydraulic conductivity in Aspen (*Populus tremuloides*) was documented one year after a defoliation experiment took place, which was designed to simulate carbon starvation (Anderegg and Callaway 2012). Reduced drought resistance in encroached Oregon white oak could also be related to the climate × encroachment effect (i.e., reduced positive effects of spring temperature with increased Douglas-fir encroachment). Although Oregon white oak and Douglas-fir appear to have different patterns of seasonal water use, there could be greater competition for subsurface water resources, including hydraulically lifted water, in encroached stands compared with unencroached conditions. This may also affect drought resistance in Oregon white oak. Contrary to my hypothesis, drought resistance in Douglas-fir was more related to DBH than by crowding by either competitor species group.

I hypothesized that competition factors would negatively affect drought resistance. However, the best drought resistance models for Oregon white oak included a positive relationship with oak crowding. Oak crowding on Douglas-fir drought resistance also had a positive relationship, but was not in the best model (Table 4). These findings suggest that oak crowding may aid drought resistance. Particular site conditions that support high oak crowding could also support more favorable growth during drought. However, the limited analysis that has been done at this site shows no clear differences in site conditions among the sample locations (i.e., soil type, water holding capacity, and drainage; Marshall 2017). High competition may reduce, cancel out, or mask climate effects (Sánchez-Salguero et al. 2015), or could be related to phenotypical structural change (such as increased proportion of latewood) in high competition environments that aid in drought resistance (Carnwath and Nelson 2016).

There are a few possible explanations for how oak crowding may aid drought resistance in Oregon white oak. The beneficial effect of oak crowding on drought resistance could be related to subsurface resource sharing by neighboring trees, as some oaks grow in a multistem habit with a shared root system. A related possibility is that oak-crowded conditions were associated with greater hydraulic lifting of deep water due to higher root density from neighboring oaks, which would be especially helpful during drought conditions and might also benefit Douglas-fir. A meta-analysis indicates that drought impacts may be minimized at an intermediate level of shade for drought-tolerant species especially (Holmgren et al. 2012). Compared to Douglas-fir, understory light is abundant under an Oregon white oak canopy, as evidenced by the rich understory communities that these ecosystems support (Thysell and Carey 2001; Devine et al. 2007; Livingston et al. 2016). It is therefore also possible that a denser Oregon white oak canopy helped to reduce overheating and evapotranspiration demand on crowded Oregon white oak trees during dry conditions while providing reduced, but still adequate, light for growth (Holmgren et al. 2012).

Climate Change and Management Implications

In California, climate models project increased climate volatility with increases in both drought events and extreme wet events into the mid to late 21st Century (Swain et al. 2018). Changes to the seasonality of precipitation are less clear (Cayan et al. 2008), but recent work suggests that precipitation patterns will be amplified with increased precipitation during winter months (November-March) and decreased precipitation in dry months (April-May; September-October) (Swain et al. 2018). In northwestern California, Oregon white oak and Douglas-fir were sensitive to precipitation and temperature (this study). However, Douglas-fir was more sensitive to growing-season precipitation (May-June), and Oregon white oak was more sensitive to winter precipitation (November-January). Therefore, enhanced seasonal precipitation would impact growth in Douglas-fir more than Oregon white oak. Projected increases in temperatures are more certain and expected to play an important role in future drought events, especially when coupled with low precipitation (Diffenbaugh et al. 2015; Williams et al. 2015). Temperature increases are likely to affect both species, but my results suggest that Oregon white oak may be more affected by severe drought, while Douglas-fir will be more affected by prolonged drought, including sustained increases in temperature. My results also suggest that increased temperature during spring and fall may also benefit Oregon white oak.

Trees with declining growth trends, whether from high competition, climate, or from some other factor, are more vulnerable to mortality (Pedersen 1998; Cailleret et al. 2017). While oaks tend to recover quickly from drought events (Anderegg et al. 2015), I found that the ability of Oregon white oak to resist drought was compromised by Douglas-fir encroachment. Further, I found higher amounts of Oregon white oak mortality in Douglas-fir encroached stands compared to oak only stands (Appendix A). This suggests that although Oregon white oak may be more resistant to drought and expected shifts in seasonal climate variability, competition from Douglas-fir continues to threaten this ecosystem. It is important to note that Douglas-fir is also a drought-tolerant species. Further, mortality in gymnosperms is associated with extended growth declines, while angiosperms, especially *Quercus*, are more likely to die after short-term growth declines (Cailleret et al. 2017). This means that Douglas-fir is likely to persist with low growth for an extended time period before eventual mortality (Cailleret et al. 2017), suggesting that in the short term, Oregon white oak will continue to be replaced by Douglas-fir encroachers, while in the long term Douglas-fir is less suited to the future climate.

Forest dynamics in this and other ecosystems continue to be driven more by competition than climate (Zhang et al. 2015), but the combination of both can lead to increased mortality, especially during drought (Young et al. 2017). My results suggest that reduction of Douglas-fir density will enhance the ability of Oregon white oak to resist future drought events and adapt to future climate conditions. These results present a strong case for the need for forest management to release Oregon white oak from Douglas-fir encroachers, and reintroduce low to moderate-intensity fire into these ecosystems. These actions may help Oregon white oak persist in the short term in order to play a critical role in future ecosystems. While radial growth in Oregon white oak is negatively affected by oak crowding, drought resistance of Oregon white oak appears to be positively associated with oak crowding. This facilitative effect might become increasingly important as drought becomes more frequent and severe under climate change (Bertness and Callaway 1994). Therefore, managers working to reduce Douglas-fir density in oak woodland habitats should also manage for a mixture of conspecific oak densities in order to maximize ecosystem function and resilience.

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APPENDIX A

Appendix A: Summary statistics by species and Douglas-fir encroachment group

Comparing Oregon white oak and Douglas-fir subject trees in all plots, mean Oregon white oak DBH (33.8 cm, SD = 16.3) is greater than mean Douglas-fir DBH (26.2, SD = 13.3) ($t = 3.71$, $p < 0.001$), and mean Oregon white oak height (13.0 m, SD = 3.74) is less than mean Douglas-fir height (15.8 m, SD = 6.26) ($t = 3.85$, $p < 0.0001$). Because plots were selected across a gradient of Oregon white oak encroachment by Douglas-fir, mean Douglas-fir crowding is greater for Douglas-fir (6.09, SD = 3.58) than for Oregon white oak (2.59, SD = 3.00) ($t = 7.66$, $p < 0.0001$), but there is no significant difference in oak crowding by species (4.82, SD = 2.92) (Figure 3).

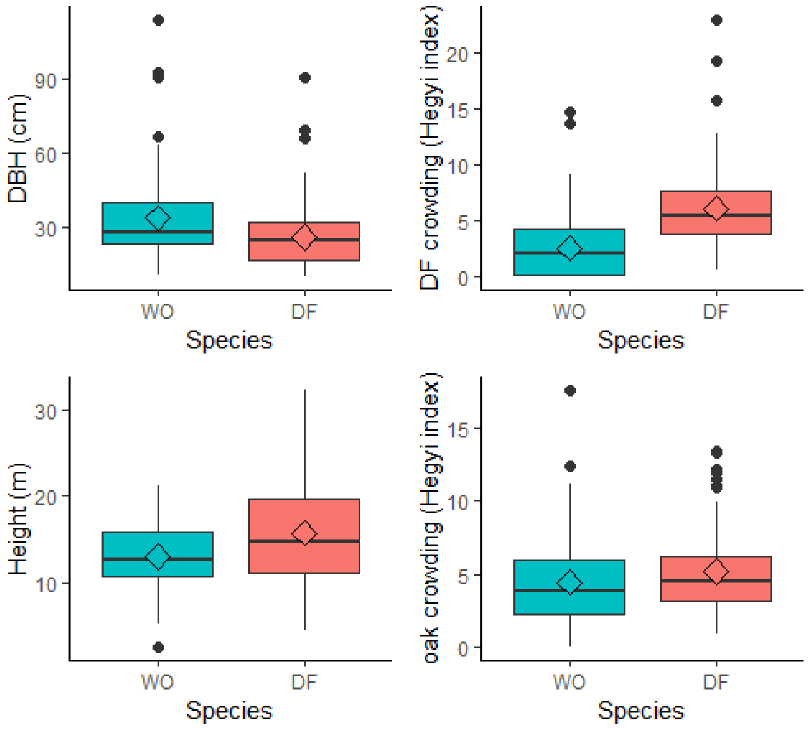


Figure 9. Boxplots of DBH (cm), height (m), Douglas-fir (DF) crowding (Hegyi index) and oak crowding (Hegyi index) for all cored trees by species (WO n=104; DF n=104).

There is no difference in mean DBH for Oregon white oak trees grouped by stand-level Douglas-fir encroachment group (33.8 cm, SD = 16.29), but mean height is less for Oregon white oak trees in oak only stands (11.6 m, SD = 3.89) than for Oregon white oak trees in Douglas-fir encroached stands (13.9 m, 3.37) (t = 3.11, p < 0.01). Douglas-fir crowding is greater for Oregon white oak trees in Douglas-fir encroached stands (3.4, SD = 2.88) than for unencroached Oregon white oak (oak only) (0.1, SD = 0.13) (t = 11.20, p < 0.0001). There is no difference in mean oak crowding by stand-level Douglas-fir encroachment group for Oregon white oak trees (4.16, SD = 3.00) (Figure 5).

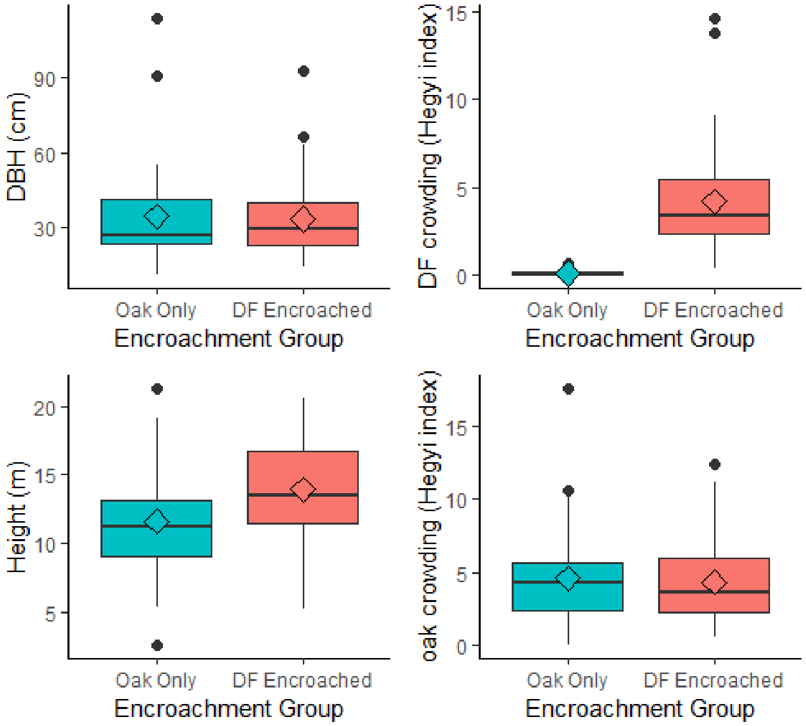


Figure 10. Boxplots of DBH (cm), height (m), Douglas-fir (DF) crowding (Hegyi index) and oak crowding (Hegyi index) for all cored Oregon white oak trees by stand-level DF encroachment group (oak only *n* = 41; Douglas-fir encroached *n* = 63).

Finally, there is a larger percentage of Oregon white oak mortality (standing dead) in Douglas-fir encroached stands than in oak only stands (21% of mapped trees versus 9% respectively). In addition, the mean DBH of standing dead Oregon white oak in Douglas-fir encroached stands (18.9 cm, SD = 9.39) is smaller than the mean DBH of standing dead Oregon white oak in oak only plots (26.9 cm, SD = 13.30) (t = 2.41, p = 0.02) (Figure 6).

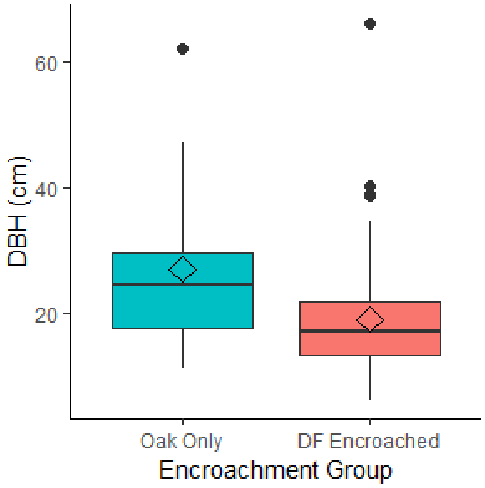
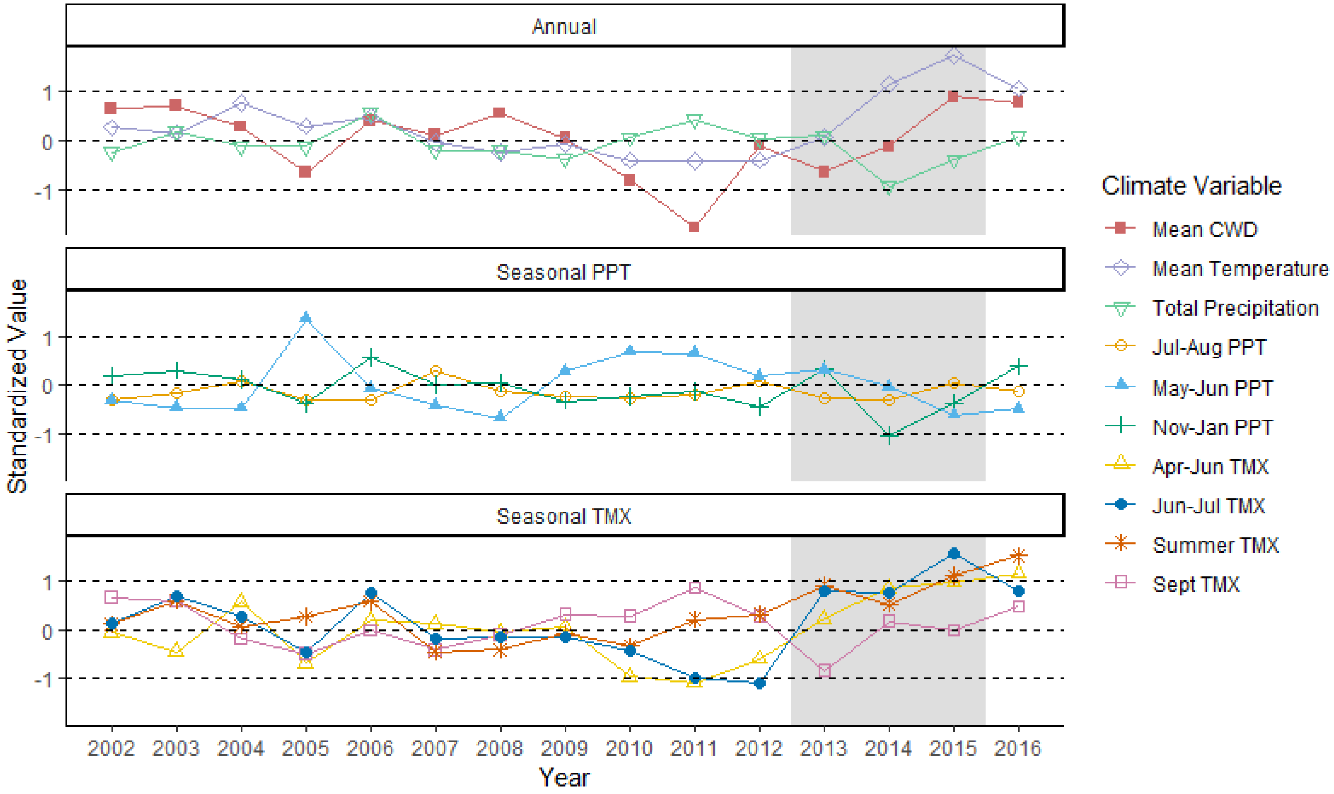


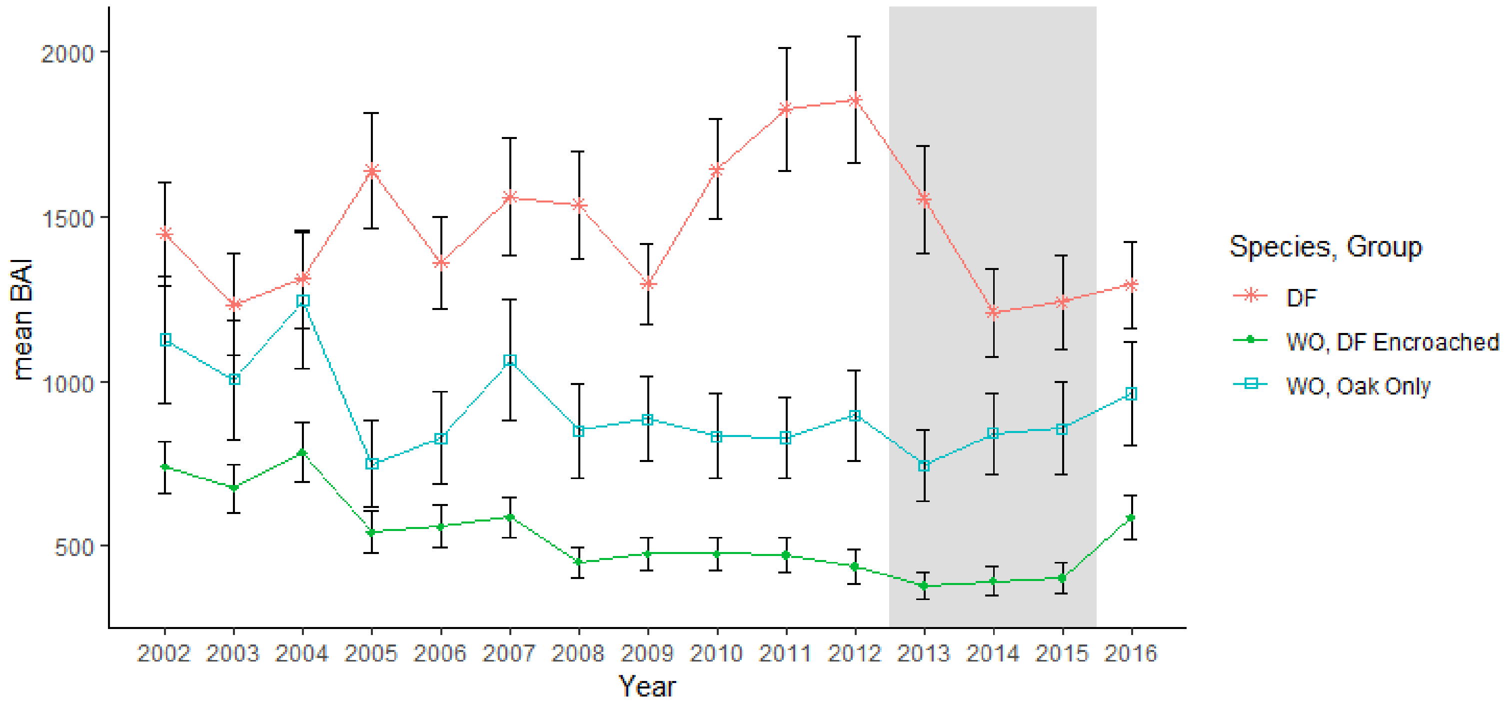
Figure 11. Boxplots of DBH (cm) for all standing dead Oregon white oak trees by stand-level DF encroachment group. Standing dead Oregon white oak accounts for 9% of mapped Oregon white oak trees (*n* = 209) in oak only plots and 21% of mapped Oregon white oak trees (*n* = 360) in Douglas-fir encroached plots.

APPENDIX B



Appendix B: Annual summary climate statistics and seasonal climate variables (Question 1) standardized relative to all data for the period 1951-2016 by subtracting the mean and dividing by two standard deviations. Mean standardized values for the Question 1 analysis period of 2002-2016 are shown. Shaded area indicates drought that occurred 2013-2015.

APPENDIX C



Appendix C: Mean basal area increment (BAI) and standard error bars for Douglas-fir (DF) and Oregon white oak (WO) by stand-level encroachment group for the analysis period (2002-2016). Shaded area indicates drought that occurred 2013-2015.