

IN THE FACE OF DROUGHT: DO FUEL TREATMENTS PROMOTE RESISTANCE
TO MULTI-YEAR DROUGHT IN A MIXED-CONIFER FOREST OF NORTHERN
CALIFORNIA?

By

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ABSTRACT

IN THE FACE OF DROUGHT: DO FUEL TREATMENTS PROMOTE RESISTANCE TO MULTI-YEAR DROUGHT IN A MIXED-CONIFER FOREST OF NORTHERN CALIFORNIA?

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Climate change is predicted to increase the frequency, duration, and severity of drought events across many bioregions. Forest managers have two active management techniques to promote resistance and resilience to drought: prescribed fire and mechanical thinning. Generally applied to reduce fuels and fire hazard, treated areas may also reduce competition for resources that may improve tree-growth during drought and reduce mortality. The recent severe and prolonged drought in California allowed me to investigate the effects of climate stress and fuel treatments on tree growth responses in a dry mixed-conifer forest ecosystem.

To assess tree-growth responses to fuel treatments during severe drought I collected and analyzed tree core samples from 300 ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) trees in the mixed-conifer forests of Whiskeytown National Recreation Area in northern California. Tree-ring data was used to investigate factors that influenced tree-growth during the study period (2008-2015). Growth was positively associated with crown ratio and negatively associated with local competition and climate water deficit (1-yr lag). Douglas-fir generally had higher annual growth than

ponderosa pine, though factors affecting growth were the same for both species. Overall, trees in thinning treatments had higher drought resistance compared to untreated stands. Drought resistance was significantly higher in treated stands compared to untreated stands during both years of extreme drought (2014-2015) for ponderosa pine but only one year (2014) for Douglas-fir. This information can help land managers decide on forest management practices that may enhance forest resistance to future drought events.

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INTRODUCTION

Greenhouse gas emissions have been associated with a steady rise in average global temperature, contributing to a general increase in climatic variability. One outcome of this trend is the predicted increase in the frequency, duration and severity of drought events in many bioregions (Settele et al. 2014, Trenberth et al. 2014, Cook et al. 2015). In forest ecosystems, drought, or a prolonged reduction of available water resources, is an important stressor that can influence tree vigor and survival. Several recent studies have linked observed increases in tree mortality to the occurrence of drought stress (e.g. Gitlin et al. 2006, van Mantgem et al. 2009, Allen et al. 2015). Trees weakened by drought stress are also more susceptible to attack from pathogens and insects, such as bark beetles (Weed et al. 2013). Prolonged periods of severe drought can lead to large-scale forest die-off, altering the structure and function of forest ecosystems (Breshears et al 2005). While reductions in available water are the primary driver of drought stress, increases in temperature can lead to higher rates of evapotranspiration that can enhance drought stress (Adams et al. 2009, Allen et al. 2015).

The widespread exclusion of fire over the last century or more has led to substantial fuel accumulation, increases in forest density, and shifts in species composition in many lower elevation, dry forests in the western US (Fulé et al. 1997, Brown et al. 2000, Safford et al. 2012). Fire exclusion is particularly an issue in dry forests that historically experienced frequent, low-severity fire regimes. In response, federal agencies have widely applied large-scale fuel reduction treatments focused on

thinning low to mid-canopy trees to reduce basal area and reducing fuels by pile burning or re-introducing fire through prescribed burns (Agee and Skinner 2005). In more recent years, forest management goals have shifted more broadly towards enhancing ecosystem resiliency for future climate conditions (USDA-FS 2011, Franklin and Johnson 2012). To assess the effectiveness of fuel treatments in this context, understanding whether management activities enhance forest resistance (remaining unaltered during disturbance) and resilience (ability to recover to pre-disturbance conditions) to disturbance events such as drought (Folke et al. 2004) is a critical need.

Tree-growth resistance to drought, or drought resistance, is an important measure of growth response to climatic stress (Lloret et al. 2011). Empirical investigations of fuel treatment impacts on drought response have yielded mixed results. While some studies focusing on ponderosa pine (*Pinus ponderosa*) have found that fuel reduction treatments can enhance tree-growth rates and improve stand resilience to disturbances such as drought (Kerhoulas et al. 2013, Thomas and Waring 2015), others have found that treatment impacts varied with tree size and time since treatment (D'Amato et al 2013). More recent studies have found that tree-growth resistance to drought was negatively related to stand density across a range of forest ecosystems, stand ages, and drought intensities (Bottero et al. 2016, Bradford and Bell 2017, Young et al. 2017). These studies suggest that tree characteristics and competition play an important role in mediating growth responses to drought stress. Trees experiencing greater competition can have reduced radial growth (Das 2012, Sánchez-Salguero et al. 2015), and in some cases,

higher probabilities of mortality (Das et al. 2011). Few studies, however, have examined the effects of competition on tree-growth under prolonged drought conditions.

The drought that recently occurred in California (2011 through 2015) was one of the most severe events in the instrumental record (Williams et al. 2015, Luo et al. 2017). Average winter season precipitation was among the driest on record, while average winter temperatures for the same period were among the highest (Seager et al. 2015). I used this natural experiment to investigate the influence of thinning and pile burning on tree-growth responses for two widespread conifer species, ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*), to the recent multi-year drought in the dry, mixed conifer forests of Whiskeytown National Recreation Area in northern California. The specific research questions examined include: 1) What factors (e.g. tree characteristics, climatic stress, competition) influence tree-growth responses during the study period (2008-2015)? 2) Do fuel reduction treatments influence forest resistance to drought stress? And 3) does drought resistance change after multiple years of extreme drought?

MATERIALS AND METHODS

Study Area

This study was conducted in the dry, mixed-conifer oak forests of Whiskeytown National Recreation Area (WNRA), located in the southeastern Klamath Mountains, approximately 13 km west of Redding, California (Figure 1). The climate in WNRA is Mediterranean, characterized by cold wet winters and warm dry summers, with a mean annual temperature of 14.4 °C (USDI 2003). Mean annual precipitation is 152 cm, falling primarily in the form of rain (USDI 2003).

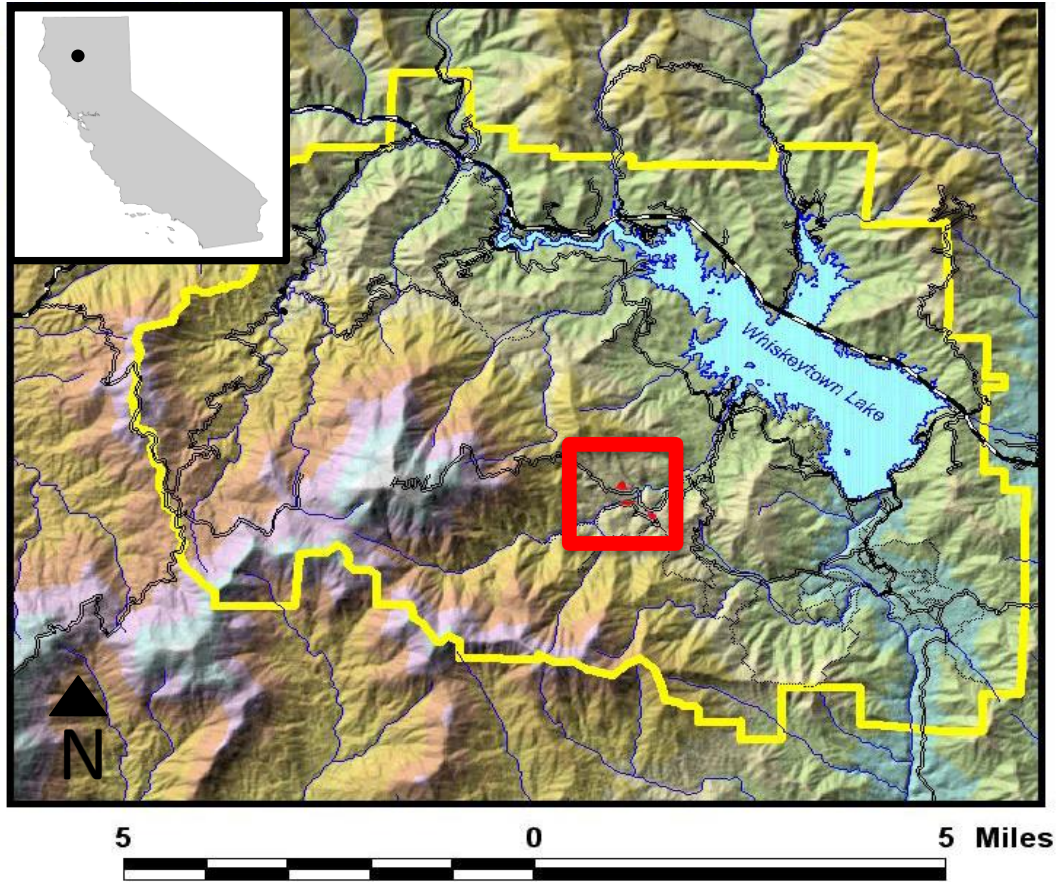


Figure 1. Study area at Whiskeytown National Recreation Area in northern California (map credit: NPS). Fuel treatment units are outlined in the red box.

WNRA was established in 1965 and encompasses 17,200 ha of forest and shrubland, including the 1,200 ha Whiskeytown reservoir, and covers a diverse range of plant communities and topography (USDI 2003). Both human and lightning ignited wildfires historically occurred in the park with fire regimes varying depending on vegetation communities, topography and human habitation (Fry and Stephens 2006). Prior to Euro-American settlement, mean fire return intervals ranged from 1.3 to 3 years in ponderosa pine-mixed conifer forests (Fry and Stephens 2006). Land-use activities of

Euro-American settlers also included mining, livestock grazing and intensive timber harvesting (Toogood 1978). Fire suppression and other disturbances have greatly reduced the frequency of fire and led to altered forest structure and composition (Leonzo and Keyes 2010). Such changes have prompted park managers to carry out fuel reduction treatments (2010) aimed at restoring historical forest structure and reducing the potential for high severity wildfire (USDI 2003). Treatments at WNRA aimed to reduce stand basal area by 30% by thinning young, conifers (< 30 cm diameter at breast height; DBH) and tanoak (*Notholithocarpus densiflorus*) while maintaining hardwood diversity (e.g. *Quercus kelloggii*, *Quercus chrysolepis*, *Acer macrophyllum*) and promoting residual conifer vigor through crown release. Thinning was conducted in 2010 with a feller-buncher and harvested material was removed using a rubber-tired skidder. Residual fuels were subsequently piled and burned in the winter of 2011.

Field Sampling

In 2016, 307 tree core samples were taken at 30 cm above the soil surface from Douglas-fir and ponderosa pine trees. Approximately 70 individuals of each species (DBH > 30 cm) were randomly sampled from three paired (treated and untreated) stands of similar composition. A 15 m fixed-radius competition plot was established around each focal (cored) tree. Species, DBH and distance from the focal tree were measured for all trees greater than 2.5 cm DBH within 5 m and all trees greater than 5 cm DBH within 15 m of each focal tree.

Sample Processing

Tree cores were prepared, dated and measured using standard dendrochronological methods (Pilcher 1990). Tree-ring chronologies were visually cross-dated and potential errors were detected using COFECHA (Holmes 1983). Only tree cores that were confidently cross-dated were used for statistical analysis. Ring-width series were converted to annual basal area increment (BAI) using the diameter inside bark at coring height and the width of each ring from the outermost ring towards the pith using the dplR package in R statistical software (Bunn 2008, R Development Core Team 2016). Tree age was estimated by counting rings from bark to pith. For cores that missed the pith but passed through the bole center, Duncan's method was used to estimate tree age (Duncan 1989). Tree age did not have a significant influence on growth and was excluded in the final analyses.

A tree-to-tree competition index (CI) was calculated for each focal tree using a distance dependent equation that takes into account the number and size of nearby trees (Hegyi 1974):

$$CI = \sum_j (DBH_j / DBH_i) / dist_{ij}$$

where DBH_i is the subject tree's DBH (cm), DBH_j is the neighbor tree's DBH and $dist_{ij}$ is the distance (m) between the focal tree and neighbor tree. A preliminary analysis that compared the competition indices of each focal tree based on three different plot sizes (radius = 10, 12.5, and 15 m) was conducted to determine which correlated best with BAI. A competition radius of 12.5 m had the highest correlation with BAI and was used

for subsequent analyses. In addition, a comparison of the effect of intra vs. inter-specific competition on growth was conducted to determine the relative importance of different types of competition. For ponderosa pine, inter-specific competition had higher correlation with BAI, while intra-specific competition had a higher correlation for Douglas-fir. This is likely due to the abundance of young Douglas-fir trees in the study area. I chose to use a competition index based on all competitors for analysis because it had the second highest correlation with BAI for both species.

Climate Data

Daily climate data from the Shasta Dam weather station (18 km NNE of the research site) for the period 1985-2015 was acquired from the Western Regional Climate Center (WRCC 2017). Missing entries in the record were interpolated from recorded values based on the day of year average using the 'ReadInputs' function in R (Guo and Westra 2016). Daily values of minimum and maximum temperature ($^{\circ}\text{C}$) were used to calculate mean daily temperature and daily precipitation values (mm) were summed for each month. Monthly potential evapotranspiration (PET) was calculated according to the Hargreaves formulation using the 'hargreaves' function (Beguería and Vicente-Serrano 2013). Monthly actual evapotranspiration (AET) was estimated from the climate data following a modified Thornthwaite-Mather water balance calculation (Dobrowski et al. 2013) and used to estimate the climatic water deficit ($\text{CWD} = \text{PET} - \text{AET}$) (Stephenson 1998). I chose these formulations of CWD because they required fewer assumptions about wind speed and insolation and provided a sufficient estimate of regional PET and

AET. For all water balance calculations a soil available water capacity value of 70 mm and latitude of 40.72° were used (Miller and White 1998). All values were then summed to the water year (Oct-Sept). In a preliminary analysis, I found tree growth to be more strongly correlated with a one year lagged Hargreaves formulation of CWD than values for the current year or values based on a Thornthwaite formulation using linear regression. Thus, a one year lagged CWD was used for analysis. Extreme drought years were characterized as those with annual CWD values greater than one standard deviation above the 30-yr mean (1985-2015). Both 2014 and 2015 were identified as extreme drought years.

Statistical Analysis

I chose a study period of 2008-2015 to evaluate treatment and drought effects on growth trends for individual trees. I fit a linear mixed-effects (LME) model for BAI ($n = 2388$; 299 focal trees with 8 observations for each with the exception of 4 trees that had missing rings in 2015) using the nlme package (R Development Core Team 2010). To determine the random-effect structure, I fit several “beyond optimal” models with different combinations of random variables and used Akaike Information Criteria (AIC) to select the simplest model with the most explanatory power (Zuur et al. 2009). I chose a model that included a random intercept for individual trees nested within site to address unaccounted variation in site conditions and tree characteristics. I then fit a series of LME models with different explanatory variables, including interaction terms, and compared the models using AIC. Models within 2 AIC units of the lowest scoring model were

considered candidates from which the final model was chosen. All final models were chosen from candidates based on lowest AIC value and whether additional estimated parameters in competing models had 95% confidence intervals that overlapped zero. All growth models included a log transformation of the response variable to address normality assumptions and the residuals were checked to ensure homoscedasticity. A first-order auto-correlation term was also included to address temporal auto-correlation in the model (Pinheiro and Bates 2000). For all statistical analyses significance was determined at $\alpha = 0.05$.

To evaluate the treatment effect on Douglas-fir and ponderosa pine I calculated mean drought resistance for all recent drought years (2012-2015) using 2011 as the pre-drought reference and divided the mean BAI during drought by the mean BAI pre-drought (Lloret et al. 2011). Calculating drought resistance in 2014 and 2015 allowed me to evaluate the effect of persistent (3 and 4 years into drought) and extreme climatic stress on drought resistance. I tested for treatment and species effects using a two-way analysis of variance (ANOVA) that included a linear mixed-model to account for site-level variation and a log transformation of drought resistance to meet normality assumptions. I used Tukey's adjustment for multiple comparisons to test for species-level differences in drought resistance. In addition, a LME model of drought resistance selected based on AIC was used to investigate factors that contributed to drought resistance during the extreme drought year 2015.

RESULTS

Stand Conditions

Tree and stand conditions varied by species and treatment (Appendix A). For ponderosa pine and Douglas-fir mean focal DBH ranged from 48.0 to 57.8 cm and 42.1 to 53.1 cm, respectively. Mean stand-level basal area was 43% lower in treated stands (23.8 – 31.6 m² ha⁻¹) compared to untreated stands (48.3 – 52.9 m² ha⁻¹). Mean stand-level competition index was 59% lower in treated stands (1.5 – 1.7) compared to untreated stands (3.1 - 4.7). Mean tree age varied between species, 103 years for ponderosa pine and 69 years for Douglas-fir, but was similar across units and treatments.

Factors Influencing Tree Growth

Mean annual BAI by tree species and treatment changed over the study period (2008-2015) in relation to CWD (Figure 2). Estimates of annual CWD ranged from 339.6 (wet years) to 832.1 mm yr⁻¹ (dry years), and began to steadily increase beginning in 2012. A decline in growth during the drought period is evident for both species, especially Douglas-fir, beginning in 2013 (lagged) following the onset of drought conditions.

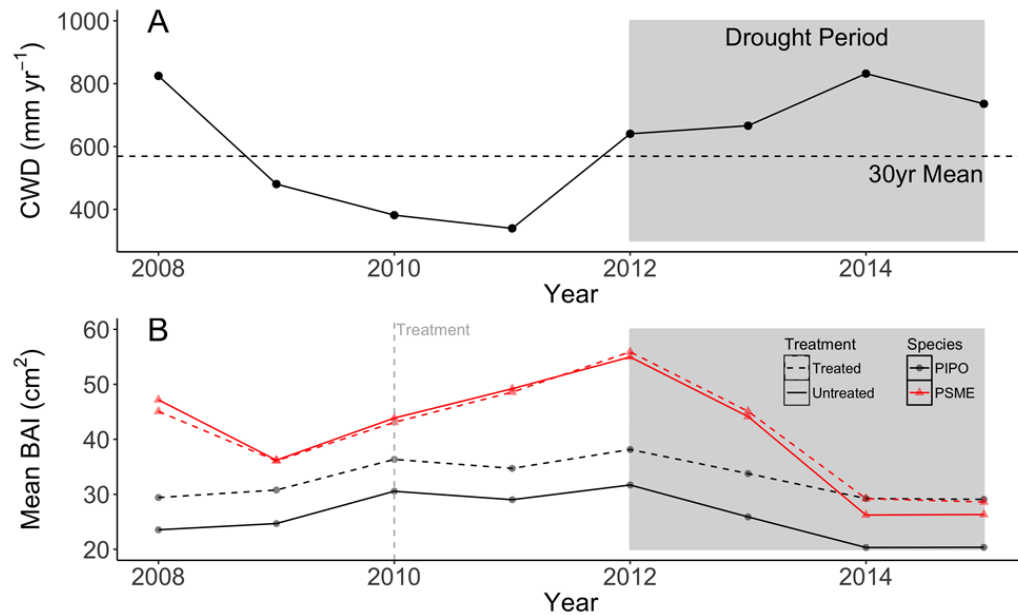


Figure 2. Time series (2008-2015) showing annual climatic water deficit (CWD) (A), and mean annual basal area increment (BAI) for ponderosa pine (black lines) and Douglas-fir (red lines) trees in treated (dashed) and untreated (solid) stands (B). Vertical dashed line represents year of thinning treatment in 2010. Gray area indicates the onset and length of drought.

Linear mixed-effect model results indicated that tree BAI (2008-2015) was associated with crown ratio, CWD (1-yr lag), competition, and species (Table 1). Trees with higher crown ratios had higher annual growth rates ($t = 3.25$, $P = 0.001$). Climate water deficit (1-yr lag) had a negative effect on annual basal area increment ($t = -17.77$; $P < 0.001$; Table 1). In general, Douglas-fir trees had higher annual growth than ponderosa pine ($t = 5.34$; $P < 0.001$; Figure 2) with the exception of persistent (3rd and 4th consecutive) and extreme drought years (2014-2015). Competition was negatively associated with growth ($t = -3.73$; $P < .001$). Individual-level tree characteristics and CWD explained a relatively low amount of the variation in BAI (marginal $R^2 = 0.19$),

while the nested effect of individual tree within site improved the final model

(conditional $R^2 = 0.71$; Table 2).

Table 1. Parameter estimates and variation for the top linear mixed-effect model of Douglas-fir and ponderosa pine growth from 2008-2015. Model parameters include crown ratio (CR), one-year lagged climatic water deficit (CWD_1), competition index (Comp) and species (SpeciesPSME). Species differences are shown relative to ponderosa pine. Estimates are shown on the log-scale. Parameter 95% confidence intervals (CI) estimated from 1000 bootstrapped samples.

Term	Estimate	Standard Error	CI
CR	1.543	0.475	0.65 to 2.55
CWD_1	-0.001	0.00004	-0.0009 to -0.0008
Comp	-0.119	0.032	-0.19 to -0.06
SpeciesPSME	0.352	0.066	0.22 to 0.47

Table 2. Top linear mixed-effects models for growth from 2008-2015 for Douglas-fir and ponderosa pine including crown ratio (CR), climatic water deficit (CWD_1), competition (Comp), diameter at breast height (DBH), height (Ht), and species using AIC. Models with $< 2 \Delta AIC$ from lowest were considered final candidate models.

Model Predictors	df	AIC	ΔAIC	AIC wt
CR, CWD_1, Comp, Species	9	1803.2	0.0	0.36
CR, CWD_1, Comp, Species, Comp*CWD_1	10	1804.2	1.0	0.22
CR, DBH, Ht, CWD_1, Comp, Species	11	1804.4	1.2	0.20
CR, DBH, CWD_1, Comp, Species	10	1805.2	2.0	0.14
CR, DBH, CWD_1, Comp, Species, Comp*CWD_1	11	1806.2	3.0	0.08
DBH, CWD_1, Comp, Species	11	1813.4	10.2	0.00
CR, DBH, Species	8	2099.2	296.0	0.00
CR, Species	7	2100.1	296.9	0.00

Drought Resistance

In general, as drought conditions persisted, drought resistance declined in both treated and untreated stands, while differences between treated and untreated stands continued to increase. In the extreme drought years of 2014-2015 (drought years 3-4), I found evidence of stand-level treatment (2014: $F = 20.9$; $P = 0.01$; 2015: $F = 15.6$; $P = 0.017$) and species (2014: $F = 34.2$; $P < 0.001$; 2015: $F = 15.5$; $P < 0.001$) effects. Median drought resistance during 2014 was estimated to be 23% higher (95% CI: 4%-45%) for

Douglas-fir (df = 4, t-ratio = -3.36; Tukey-adjusted $P = 0.028$) and 23% higher (95% CI: 3%-46%) for ponderosa pine (df = 4, t-ratio = -3.26; Tukey-adjusted $P = 0.031$) in treated compared to untreated stands (Figure 3). Median species-level drought resistance in 2015 for ponderosa pine (df = 4, t-ratio = -3.10; Tukey-adjusted $P = 0.036$) in treated stands was estimated to be 30% (95% CI: 3% - 64%) higher compared to untreated stands, and was nearly significantly different for Douglas-fir (df = 4, t-ratio = -2.67; Tukey-adjusted $P = 0.056$) (Figure 3).

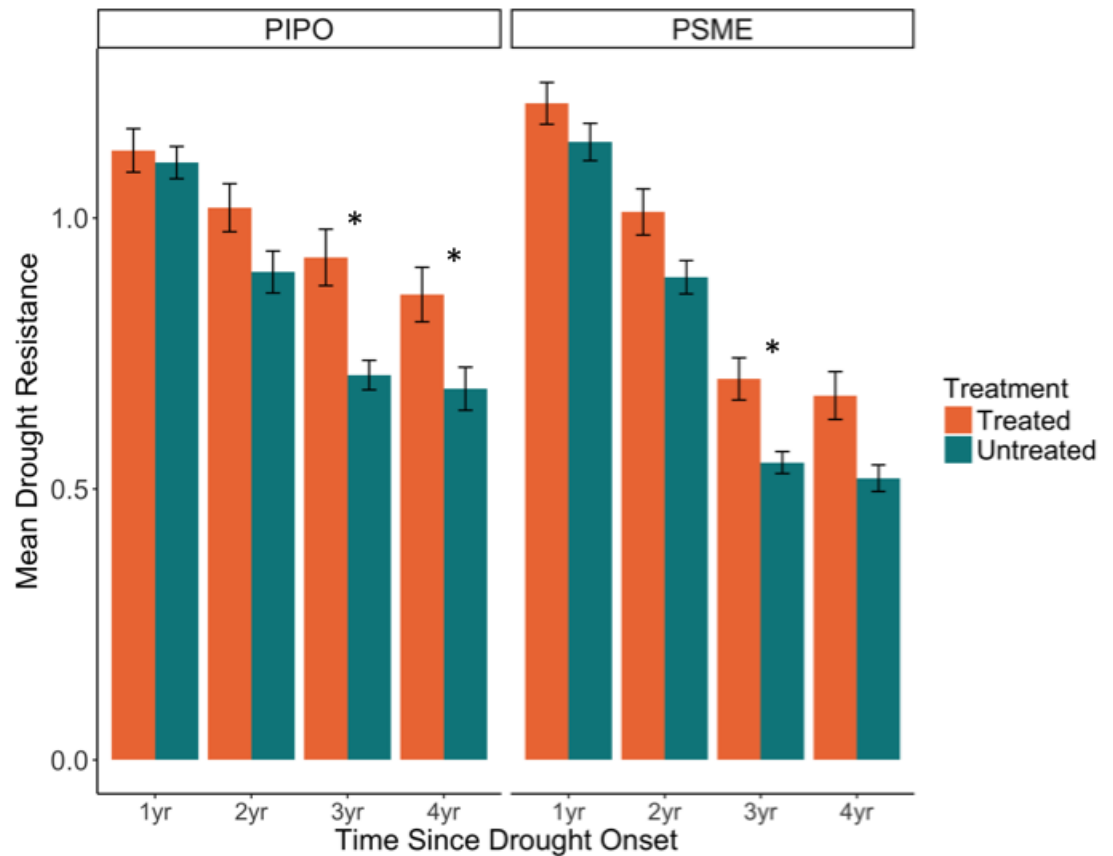


Figure 3. Mean drought resistance by species (PIPO = ponderosa pine, PSME = Douglas-fir) for several drought years beginning in 2012 (1yr). Asterisks denote Tukey-adjusted significant species-level treatment differences ($\alpha = 0.05$) for drought year on the log-scale.

Linear mixed-effect model results indicated that drought resistance during the extreme and persistent drought year of 2015 (drought year 4) was negatively associated with DBH, competition, and species (Table 3). Larger trees had lower drought resistance compared to smaller trees ($t = -2.72$; $P = 0.007$). Trees experiencing higher competition had reduced drought resistance ($t = -2.81$; $P = 0.005$; Figure 4). In general, Douglas-fir had lower drought resistance than ponderosa pine in drought year 4 ($t = -4.31$; $P < 0.001$). Factors included in the final model explained a low amount of variability in drought resistance (marginal $R^2 = 0.08$), and the random intercept for site only slightly improved the model (conditional $R^2 = 0.09$; Table 4).

Table 3. Model parameter estimates and variation for top model of individual tree characteristics influencing drought resistance of Douglas-fir and ponderosa pine in drought year 2015. Model parameters include: diameter at breast height (DBH), competition index (Comp) and species. Species differences are shown relative to ponderosa pine. Estimates are shown on the log-scale. Parameter 95% confidence intervals (CI) estimated from 1000 bootstrapped samples.

Term	Estimate	Standard Error	CI
DBH	-0.01	0.002	-0.01 to -0.002
Comp	-0.06	0.021	-0.10 to -0.02
SpeciesPSME	-0.26	0.061	-0.39 to -0.14

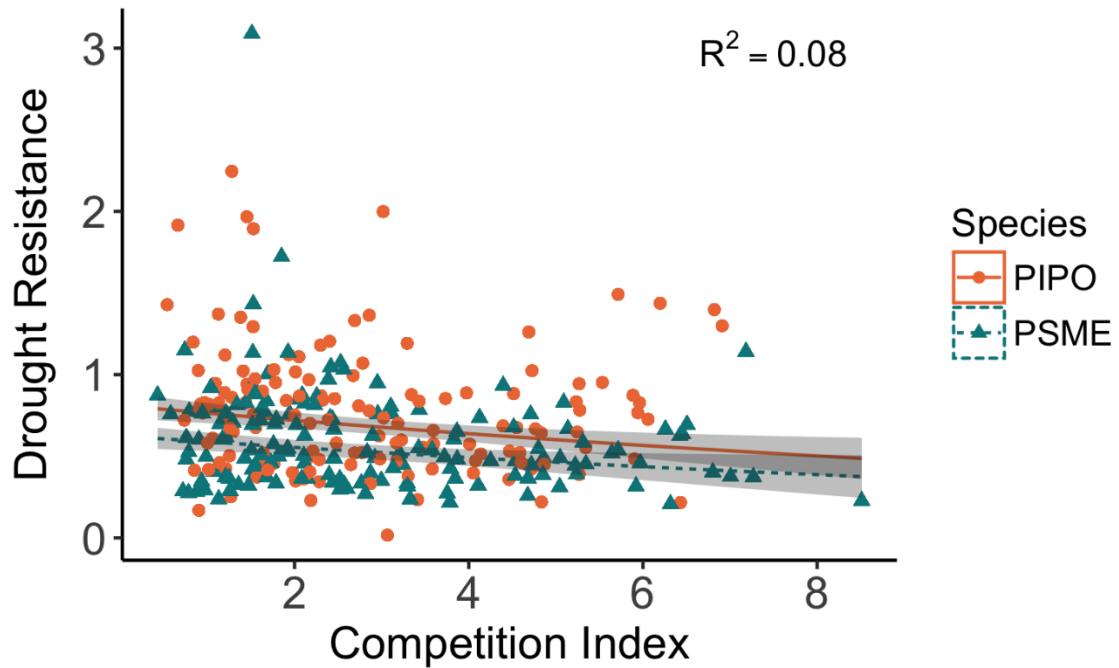


Figure 4. Mean global prediction lines for drought resistance in drought year 4 (2015) in response to competition with standard error for ponderosa pine and Douglas-fir from linear mixed-effects model. Scatter plot shows actual drought resistance values.

Table 4. Selection of linear mixed-effects model for drought resistance in drought year 4 (2015) for Douglas-fir and ponderosa pine including crown ratio (CR), competition (Hegyi12.5), diameter at breast height (DBH), height (Ht), and species using AIC. Models with < 2 ΔAIC from lowest were considered final candidate models.

Model Predictors	df	AIC	ΔAIC	AIC wt
DBH, Hegyi12.5, Species	6	444.0	0.0	0.51
CR, DBH, Ht, Hegyi12.5, Species	8	445.2	1.2	0.28
CR, DBH, Hegyi12.5, Species	7	446.0	2.0	0.19
CR, Hegyi12.5, Species	6	450.2	6.2	0.02

DISCUSSION

Factors Influencing Tree Growth

A combination of tree-level (crown ratio and competition) and regional climate (CWD) factors contributed to variability in growth of both conifer species over the study period (2008-2015). Crown ratio, a measure of individual tree vigor (Sprinz and Burkhart 1987, Hasenauer and Monserud 1996), was found to be a more important predictor of radial growth than other individual tree characteristics such as DBH, height and tree age. While there may be a relationship between tree size and vigor (e.g. large trees have greater access to light and water), crown ratio estimates may serve as a more direct proxy of photosynthetic potential and thus growth. Previous studies have shown that thinning activities may lead to increases in the crown ratios of understory trees (e.g., Bailey and Tappeiner 1998), which may improve growth during periods of climatic stress. Likewise, trees with lower competition were found to be growing faster on average than trees with higher competition, similar to other studies (e.g., Das 2012, Sánchez-Salguero et al. 2015). Thinning activities can also reduce precipitation interception (Kohler et al. 2010), increase available soil moisture, and increase light availability (Gray et al. 2002), all of which can help stimulate plant growth.

Similar to other studies, I found that species-level growth responses to climatic stress vary and can have multi-year lagged effects (e.g. Bréda et al. 2006, Hurteau et al. 2007). Understanding this lagged response to climatic stress is important when

interpreting growth responses to successive years of drought stress. Trees have a number of ways of coping with stressful short-term climate conditions such as accessing deep soil water, stomatal regulation, or utilization of carbon reserves (McDowell et al. 2008). Under successive years of stressful conditions, these coping strategies can be exhausted resulting in low growth periods (Bréda et al. 2006).

Species-level differences in growth may be useful in explaining differential responses to drought stress and fuel treatments. Throughout most of the study period, Douglas-fir had a higher annual growth rate than ponderosa pine despite the fact that Douglas-fir trees were generally younger and smaller. However, during the extreme drought years 2014-2015, annual growth for the two species was similar. Differences in morphology (e.g. leaf area) and physiological strategies may explain the observed variation in growth rates between the two species. A study comparing leaf morphology and physiological responses to light between species found that Douglas-fir had greater leaf mass per area than ponderosa pine which is likely associated with greater photosynthetic capacity (Bond et al. 1999).

Drought Resistance

My results suggest that fuel reduction treatments may help to promote drought resistance in mixed-conifer forests of WNRA, however, it is highly dependent on treatment intensity, drought persistence, tree characteristics and species. In general, these findings are consistent with other recent studies that found a positive effect of thinning treatments on drought resistance (Kohler et al. 2010, D'Amato et al. 2013, Bottero et al.

2016). In addition, lower stand basal area (Young et al. 2017) and fuel reduction treatments have been associated with lower mortality probabilities for some species during drought events (Collins et al. 2014, van Mantgem et al. 2016). The potential to realize these benefits, however, depends upon individual tree characteristics (e.g. tree size). Similar to studies in the Sierra Nevada and Southwestern US, DBH at WNRA was found to be negatively associated with drought resistance, perhaps due to higher water demand for larger trees (D'Amato et al. 2013, McDowell and Allen 2015). This result contrasts with studies in the Southwest where drought resistance was greater in larger diameter ponderosa pine (Kerhoulas et al. 2013). This suggests tree and site characteristics are important for how trees respond, and generalizations across a given species are not appropriate outside of the geographic context.

Competition continued to be a driver of drought resistance during periods of extreme climatic stress (also see Sánchez-Salguero et al. 2015). Reducing competition for resources can increase the availability of resources that support more rapid growth (Latham and Tappeiner 2002, McDowell et al. 2006) and may improve water use efficiency (McDowell et al. 2006). On the other hand, competition has also been found to be less influential on growth during stressful periods (Kunstler et al. 2011, Carnwath and Nelson 2016, Ford et al. 2016). While greater access to solar radiation may improve growing conditions in more mesic forest types (Ford et al. 2016), projected temperature increases and changes in inter-annual precipitation are more likely to negatively affect tree growth and survival in drought-prone areas (Allen et al. 2015). High competition, therefore, may exacerbate the effects of drought in dry forest types similar to those at

WNRA. The low variability explained by the drought resistance model suggests that other factors are also important in explaining variability in drought resistance.

Although drought resistance was improved in treated stands at WNRA during extreme drought years, Douglas-fir may still be more vulnerable to the impact of drought than ponderosa pine. During the two years of persistent and extreme drought (2014-2015), Douglas-fir had lower mean resistance in treated and control stands compared to ponderosa pine. Increased drought sensitivity may be related to greater leaf area (McDowell and Allen 2015) and the observed variability in Douglas-fir growth pattern throughout the study period (Ogle et al. 2000, Fekedulegn et al. 2003). Other studies have linked low-growth periods (Cailleret et al. 2016) and sharp declines in growth with an increased probability of mortality (Das et al. 2007). Ponderosa pine, on the other hand, was generally less sensitive to drought stress (i.e. less change in growth rate). In persistent and extreme drought years (2014-2015) ponderosa pine showed a significant positive response to thinning treatments, while Douglas-fir had a mixed response. Although ponderosa pine had higher drought tolerance relative to Douglas-fir and stronger response to treatments, in the face of climate uncertainty, it may be best to manage for forest diversity (all native species) to bet hedge against varied responses to extreme drought and other disturbance (e.g. bark beetle) events (Millar and Stephenson 2015).

Despite the detection of differences in drought resistance between treated and untreated stands, my results were not strongly significant. One explanation for the lack of strong results could be that fuel treatments at WNRA reduced only 34% of live BA, a

light thin by some standards, and in some cases left nearby competitor trees to retain species diversity (i.e. conifer and native oak species). The benefits of thinning vary with intensity of treatment (e.g. Kohler et al. 2010, Kerhoulas et al. 2013, Bottero et al 2016, Sohn et al. 2016a). For example, Kerhoulas et al. (2013) found that dry-year growth was maintained at pre-dry-year levels after both moderate and heavy thinning treatments, but decreased in the light thinning and control groups for ponderosa pine in the Southwest. It is possible that more intensive thinning at WNRA would have resulted in more substantial growth benefits during the recent drought. These results can help managers plan thinning levels to maximize treatment benefits for drought mitigation and species responses.

Time since treatment in relation to a disturbance event is also an important factor in post-treatment growth response (Latham and Tappeiner 2002, Sohn et al. 2016b). In WNRA, fuel reduction treatments were completed two years before the onset of the drought. Large mature trees can have a delayed release from thinning (Latham and Tappeiner 2002, Kerhoulas et al. 2013), and forests at WNRA may not have been physiologically capable of taking advantage of additional growing space in the short-term. Potential growth benefits from the treatments were also likely limited by the poor growing conditions during the drought. In WNRA, mean stand-level resistance declined in both treated and control stands throughout the 4-yr drought period, while the difference in resistance between the treated and untreated stands increased.

Perhaps the most important evaluation of fuel treatment efficacy is forest drought resilience (Millar et al. 2007). Forest drought resilience is a measure of longer-term

growth responses to drought events (Lloret et al. 2011). Since samples were taken while California was still in a drought, I was unable to evaluate the subsequent recovery of forests from drought stress. Given the uncertainty in climate projections, monitoring and adaptively managing forest stand conditions may be our best approach to mitigating the impacts of a changing climate (Millar et al. 2007, Franklin and Johnson 2012, Bradford and Bell 2017). A future study could evaluate whether the modest gains in resistance observed at WNRA translate to longer-term improvements in growth.

Overall, I found individual tree characteristics, local competition and climatic stress to be important drivers of tree growth during the study period (2008-2015). Additionally, my results suggest that reducing stand density, and thus competition, can improve tree and stand-level drought resistance during extreme drought. However, these benefits are dependent upon tree characteristics, thinning intensity, drought severity and species-level responses. Understanding species-level differences in both drought sensitivity and treatment response can help managers plan future treatments. In the face of climate uncertainty, it will be critical for managers to evaluate treatment effects and be prepared to adapt future prescriptions to changing conditions.

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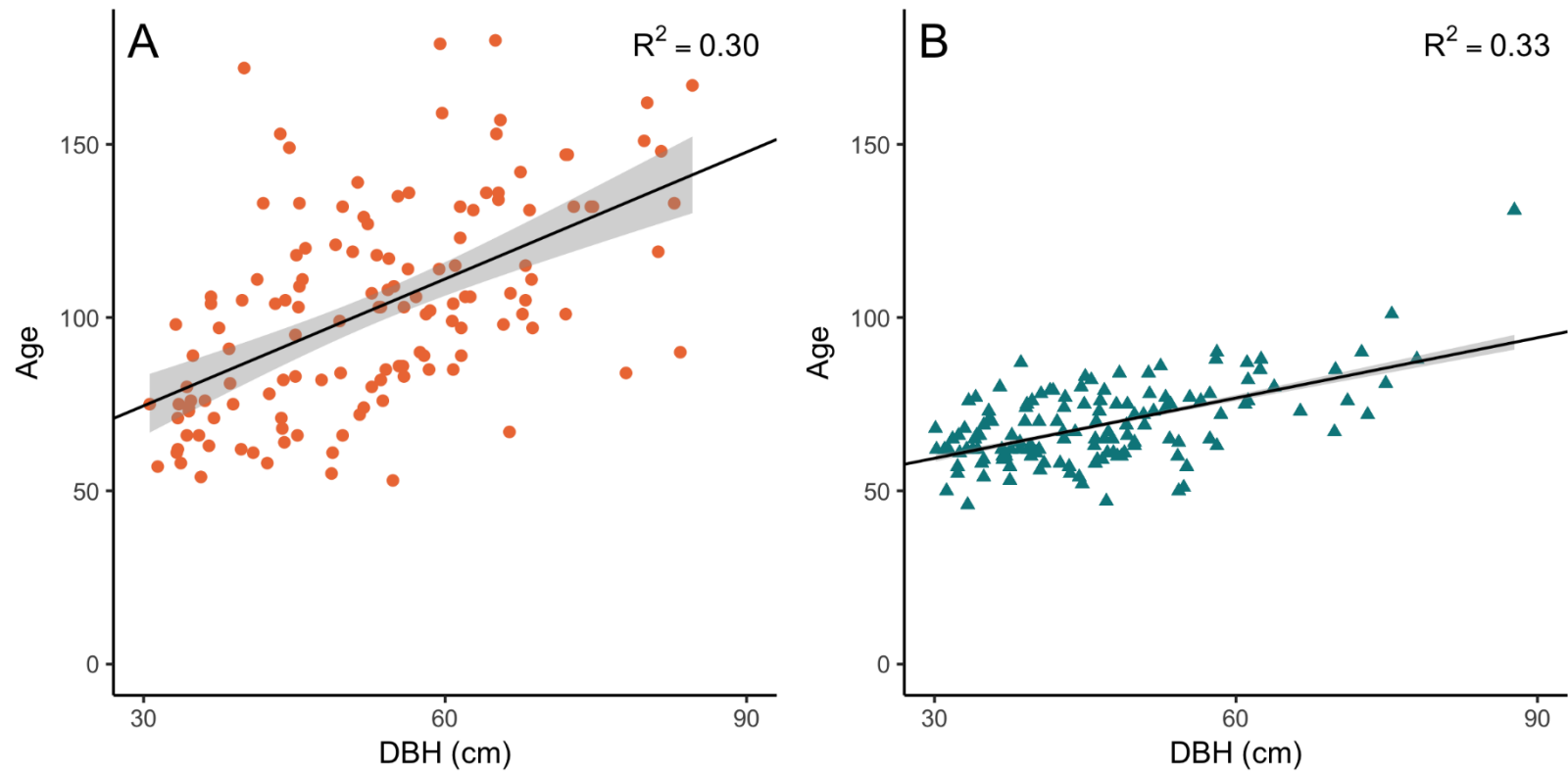
APPENDIX A

Appendix A: Summary statistics for treated and untreated stands at WNRA. Mean values (± 1 standard deviation) are shown for focal tree diameter at breast height (DBH), stand-level basal area, tree age and competition index. Treated stands were thinned from below with a goal of reducing stand basal area by 30%.

Site	No. of Focal Trees PIPO/PSME	Focal DBH (cm) PIPO/PSME	Basal Area (m ² ha ⁻¹)	Tree Age PIPO/PSME	Competition Index
Treated D	25/23	56.0 \pm 11.4/53.1 \pm 16.4	31.7 \pm 5.3	97.1 \pm 25.7/70.1 \pm 10.9	1.5 \pm 0.7
Treated F	25/24	48.0 \pm 12.3/47.9 \pm 7.0	23.8 \pm 6.7	92.8 \pm 28.8/69.3 \pm 6.5	1.7 \pm 0.5
Treated G	22/32	56.8 \pm 13.4/47.3 \pm 13.3	31.3 \pm 8.3	118.9 \pm 21.6/70.1 \pm 11.7	1.7 \pm 0.7
Untreated D	25/24	57.8 \pm 17.2/52.0 \pm 15.8	50.3 \pm 11.2	101 \pm 17.9/75.3 \pm 10.7	3.1 \pm 1.2
Untreated F	25/25	52.1 \pm 15.4/42.1 \pm 8.2	48.3 \pm 9.6	116.7 \pm 33.7/66.6 \pm 6.1	4.3 \pm 1.5
Untreated G	24/25	51.9 \pm 14.0/45.1 \pm 12.0	52.7 \pm 11.3	92.9 \pm 36.6/62.7 \pm 16.8	4.7 \pm 1.3

APPENDIX B

Appendix B: Scatter plot of tree size (DBH) and age relationship for ponderosa pine (A) and Douglas-fir (B). Fitted line generated from species-specific linear models predicting age from DBH with 95% confidence interval.



APPENDIX C

Appendix C: 30-year (1985-2015) mean growth trends for ponderosa pine and Douglas-fir in treated and untreated stands. Gray box represents the recent drought period (2012-2015).

