

Thinning, tree-growth, and resistance to multi-year drought in a mixed-conifer forest of northern California

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ABSTRACT

Drought is an important stressor in forest ecosystems that can influence tree vigor and survival. In the U.S., forest managers use two primary management techniques to promote resistance and resilience to drought: prescribed fire and mechanical thinning. Generally applied to reduce fuels and fire hazard, treatments may also reduce competition for resources that may improve tree-growth and reduce mortality during drought. A recent severe and prolonged drought in California provided a natural experiment to investigate tree-growth responses to fuel treatments and climatic stress. We assessed tree-growth from 299 ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) in treated and untreated stands during severe drought from 2012 to 2015 in the mixed-conifer forests of Whiskeytown National Recreation Area (WNRA) in northern California. The treatment implemented at WNRA removed 34% of live basal area through mechanical thinning with a subsequent pile burning of residual fuels. Tree-growth was positively associated with crown ratio and negatively associated with competition and a 1-year lag of climate water deficit, an index of drought. Douglas-fir generally had higher annual growth than ponderosa pine, although factors affecting growth were the same for both species. Drought resistance, expressed as the ratio between mean growth during drought and mean growth pre-drought, was higher in treated stands compared to untreated stands during both years of severe drought (2014 and 2015) for ponderosa pine but only one year (2014) for Douglas-fir. Thinning improved drought resistance, but tree size, competition and species influenced this response. On-going thinning treatments focused on fuels and fire hazard reduction are likely to be effective at promoting growth and greater drought resistance in dry mixed-conifer forests. Given the likelihood of future droughts, land managers may choose to implement similar treatments to reduce potential impacts.

1. Introduction

Climate change is predicted to increase the frequency, duration and severity of drought events in many bioregions (Settle et al., 2014, Trenberth et al., 2014, Cook et al., 2015). Drought, or a prolonged reduction of available water resources, is an important stressor in forest ecosystems 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 a reduction in available water is the primary driver of drought stress, an increase in

temperature can lead to higher rates of evapotranspiration that can enhance drought stress (Adams et al., 2009, Allen et al., 2015). The impacts of drought on forests may be further exacerbated by the legacy of past land use policies and practices that resulted in substantial increases in stand density (e.g., fire exclusion; Safford et al., 2012).

In response, forest managers have applied large-scale fuel reduction treatments focused on thinning low to mid-canopy trees to reduce basal area and pile burning or prescribed burning to reduce fuels (Agee and Skinner, 2005). In recent years, forest management goals have shifted more broadly towards enhancing ecosystem resiliency under 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 is a

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critical need (Folke et al., 2004).

Tree-growth responses can effectively measure drought resistance, where resistant individuals show relatively little change in growth patterns (e.g., Lloret et al., 2011). Empirical investigations of fuel treatment impacts on growth and drought response have yielded mixed results. Fuel treatments can enhance tree-growth rates and improve resistance to short-duration droughts (1–2 years) (Kerhoulas et al., 2013, Thomas and Waring, 2015), but responses can vary with species, tree size and time since treatment (Latham and Tappeiner, 2002, D'Amato et al., 2013). In many forest ecosystems and drought conditions, higher stand density often negatively affects tree-growth and drought resistance (Bottero et al., in press, Bradford and Bell, 2017). Trees experiencing greater competition can have reduced radial growth (Das, 2012, Sánchez-Salguero et al., 2015), and in many cases, higher probabilities of mortality (Cailleret et al., 2016). Few studies, however, have directly examined the effects of competition reduction on tree-growth under prolonged and severe drought conditions.

A recent prolonged drought in California (2012 through 2015) was one of the most severe events in the instrumental record (Williams et al., 2015, Luo et al., 2017). Average winter precipitation was among the driest on record, while average winter temperatures for the same period were among the highest (Seager et al., 2015). Extensive forest mortality resulting from prolonged drought conditions was observed in the southern Sierra Nevada (Young et al., 2017). However, the impacts and responsiveness of trees in more northern locations in California (e.g. Klamath Mountains), where mortality was less severe, have not been well studied.

We used this drought event as a natural experiment to investigate the influence of thinning and pile burning on tree-growth responses for two widespread conifer species, ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), to a recent multi-year drought in dry, mixed-conifer forests of Whiskeytown National Recreation Area in the Klamath Mountain ecoregion of northern California. We analyzed our data at two different scales: individual tree and treatment-levels. For individual trees, we investigated the factors (e.g. tree characteristics, climatic stress, competition) influencing tree-growth responses during the study period (2008–2015) and the factors influencing drought resistance in 2015 (the fourth consecutive year of drought). At the treatment-level, we assessed whether thinning treatments influenced forest resistance to drought stress and how the growth response changed over successive years of severe drought. Results from our study will help land managers assess whether fuels treatments enhance forest resistance to future drought events.

2. Methods

2.1. Study area

This study was conducted in the dry, mixed-conifer forests of Whiskeytown National Recreation Area (WNRA), located in the south-eastern Klamath Mountains, approximately 13 km west of Redding, California (Fig. 1; 40.595997, -122.592651). WNRA was established in 1965 and encompasses 17,200 ha of forest and shrubland, including the 1200 ha Whiskeytown reservoir, and includes a diverse range of plant communities and topography (USDI, 2003). The climate in WNRA is Mediterranean, characterized by cool 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).

Both human and lightning ignited wildfires historically occurred in WNRA with fire regimes varying depending on vegetation communities, topography and human habitation (Fry and Stephens, 2006). Prior to Euro-American settlement, the mean fire return interval was reported to

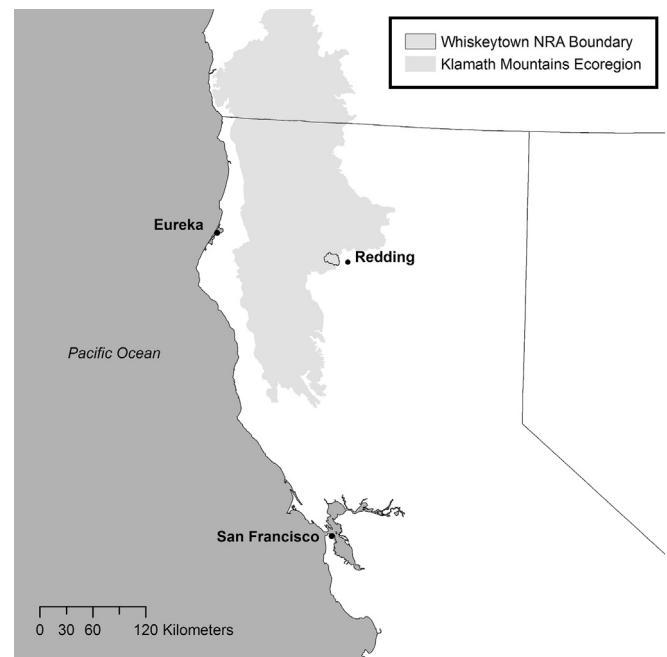


Fig. 1. Study area at Whiskeytown National Recreation Area in northern California.

range from 4.8 to 7.4 years in ponderosa pine-mixed conifer forests (Fry and Stephens, 2006). Land-use activities of Euro-American settlers 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).

These 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 reduced live basal area (BA) by 34% (based on pre-treatment data) through thinning young conifers (< 30 cm diameter at breast height; DBH) and tanoak (*Notholithocarpus densiflorus*) while maintaining other hardwood species (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. The treatment units (D, F, G) ranged in size from 0.9 to 3 ha, totaling 6.5 ha.

Tree and stand conditions varied by species and treatment (Table 1). Mean focal DBH for ponderosa pine and Douglas-fir ranged from 48.0 to 57.8 cm and 42.1 to 53.1 cm, respectively. Mean treatment-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 treatment-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.

2.2. Field data collection and sample processing

In 2016, approximately 150 Douglas-fir and ponderosa pine (focal trees) with DBH > 30 cm were sampled using random GPS points from three treated and three untreated stands of similar elevation, aspect,

Table 1

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

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

and composition. Similar site conditions in treated and untreated stands minimized unmeasured site differences when assessing for treatment effects. Tree core samples were taken from 307 focal trees at 30 cm above the soil surface. Characteristics including tree height, height to live crown, shrub cover in 5 m circular plots, and DBH were recorded for each focal tree. Tree height and height to live crown were used to calculate crown ratio. We chose to measure these tree characteristics because of their association with tree-growth (Hasenauer and Monserud, 1996) and drought resistance (McDowell and Allen, 2015). In a preliminary analysis, we found that shrub cover did not have a significant influence on tree-growth and thus we did not include it in further analyses. Competition was measured using a 15 m fixed-radius plot centered 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.

Tree cores were sanded, mounted, visually dated, and measured with WinDENDRO (Reg 2014a; Regent Instruments Inc. Quebec, Canada) following standard dendrochronological methods (Pilcher, 1990). Tree-ring chronologies were cross-dated with potential errors detected using the computer program COFECHA (Holmes, 1983). Only tree cores that were confidently cross-dated were used for statistical analysis (299 of 307 cored trees). Ring-width series were converted to annual basal area increment (BAI, cm² yr⁻¹) 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 (Bunn, 2008) in R statistical software (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 (1989) method was used to estimate the number of rings to pith. However, the final analysis excluded tree age because it did not have a significant influence on growth.

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

$$\text{Comp} = \sum_j (\text{DBH}_j/\text{DBH}_i)/\text{dist}_{ij}$$

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 plot size correlated best with BAI over the period 2008–2015. This analysis ensured that the plot radius captured nearby competitors that had an influence on focal tree growth and excluded those that did not. 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-specific and

inter-specific competition on growth was conducted to determine the relative importance of different types of competition. Inter-specific competition had a higher correlation with BAI for ponderosa pine, while intra-specific competition had a higher correlation for Douglas-fir. These relationships are likely due to the greater abundance of young Douglas-fir trees in the study area. We chose to use a competition index based on all competitors for analysis because it had the second highest correlation with BAI for both species.

2.3. 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 from the *evapotranspiration* package in R (Guo and Westra, 2016). Daily values of minimum and maximum temperature (°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 from the *SPEI* package in R (Beguería and Vicente-Serrano, 2013). Monthly actual evapotranspiration (AET) was estimated from the climate data following Dobrowski et al. (2013), based on a soil available water capacity value of 70 mm and a latitude of 40.72° (Miller and White, 1998). Monthly climatic water deficit (CWD) was calculated by subtracting AET from PET (Stephenson, 1998) and all values were summed to the water year (Oct–Sept).

In a preliminary analysis, we found a stronger correlation between tree-growth and a one-year lagged formulation of CWD rather than values for the current year. Thus, we used a one-year lagged CWD for our statistical analysis. Two years of our study (2014 and 2015) were considered to be severe drought years based on annual CWD values greater than one standard deviation above the 30-yr mean (1985–2015).

2.4. Statistical analysis

We modeled the effect of tree characteristics, climate, and competition on individual tree growth from 2008 to 2015 by fitting a linear mixed-effects (LME) model for BAI ($n = 2388$; 299 focal trees with eight observations for each with the exception of four trees that had missing rings in 2015) using the *nlme* package (R Development Core Team, 2010). To determine the random-effect structure, we fit several "beyond optimal" models with different combinations of explanatory variables and used Akaike Information Criteria (AIC) to select the simplest model with the most explanatory power (Zuur et al., 2009). Our candidate models included a random intercept for individual trees

nested within unit to address unaccounted variation in unit conditions and tree characteristics. A series of LME models with different explanatory variables, including interaction terms (i.e. competition*CWD), were compared using AIC. Models within 2 AIC units of the lowest scoring model were considered candidates from which the final model was chosen. Final selection was made based on the model with the lowest AIC value and parameters that had 95% confidence intervals that did not overlap zero. All models included a log transformation of BAI to address assumptions and the residuals were checked to ensure normality and homoscedasticity. A first-order auto-correlation term was also included to address temporal auto-correlation in the model and was checked using ACF plots (Pinheiro and Bates, 2000). For all statistical analyses significance was determined at $\alpha = 0.05$.

To evaluate the growth response to drought for Douglas-fir and ponderosa pine in treated and untreated units, we estimated drought resistance of each sampled tree for all recent drought years (2012–2015), following Lloret et al. (2011). Drought resistance was calculated for each tree by dividing BAI during drought (for each drought year) by BAI pre-drought, with 2011 as the pre-drought reference, so that higher values indicate greater resistance to drought. Calculating drought resistance in 2014 and 2015 allowed us to evaluate the effect of persistent (3 and 4 years into drought) and severe climatic stress on drought resistance. At the treatment-level, we tested for treatment and species effects during the severe drought years 2014 and 2015 using a two-way analysis of variance (ANOVA) that included a LME model to account for unit-level variation and a log transformation of drought resistance to meet normality assumptions. A Tukey’s adjustment for multiple comparisons was used to test for species-level differences in drought resistance. In addition, a LME model of tree-level drought resistance, selected based on AIC, was used to investigate

Table 2

Top linear mixed-effects models for growth from 2008 to 2015 for Douglas-fir and ponderosa pine including crown ratio (CR), one-year lagged climatic water deficit (CWD₁), competition (Comp), diameter at breast height (DBH), height (Ht), and species using AIC. Models with < 2 Δ AIC from lowest were considered final candidate models.

Model Predictors	df	AIC	Δ AIC	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	9	1813.4	10.2	< 0.01
CR, CWD ₁ , Species	8	1814.5	11.3	< 0.01
CR, DBH, Species	8	2099.2	296.0	< 0.01
CR, Species	7	2100.1	296.9	< 0.01

factors that contributed to drought resistance during the severe drought year of 2015. We evaluated several models, including polynomials, following the criteria outlined above. All variables in both of the final models (growth and drought resistance) reported had a variable inflation factor less than 1.4, indicating that multi-collinearity was not an issue.

3. Results

3.1. Factors influencing tree growth

Mean annual BAI by tree species and treatment changed over the study period (2008–2015) in relation to CWD (Fig. 2). Estimates of

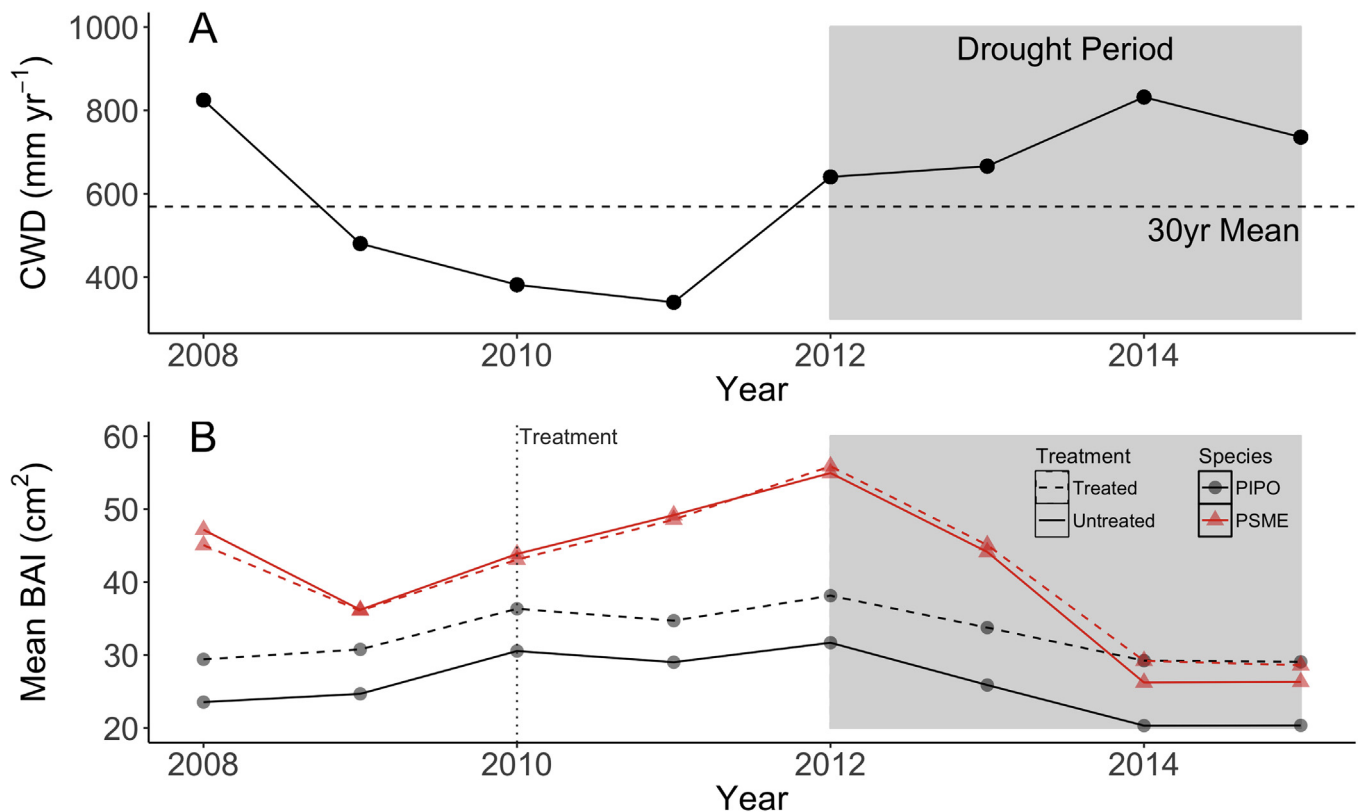


Fig. 2. Time series (2008–2015) showing (A) annual climatic water deficit (CWD), and (B) mean annual basal area increment (BAI) for ponderosa pine (PIPO) and Douglas-fir (PSME) trees in treated (dashed) and untreated (solid) stands. Vertical dashed line represents year of thinning treatment in 2010.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

Table 3

Parameter estimates and variation for the lowest AIC linear mixed-effect model of Douglas-fir and ponderosa pine growth from 2008 to 2015. Model parameters include crown ratio (CR), one-year lagged climatic water deficit (CWD₁), competition index (Comp) and species (Species). Species differences are shown relative to ponderosa pine. Estimates are shown on the log-scale. Parameter 95% confidence intervals (CI) were estimated from 1000 bootstrapped samples.

Term	Estimate	Standard Error	CI
CR	1.543	0.475	0.65–2.55
CWD ₁	−0.001	0.00004	−0.0009 to −0.0008
Comp	−0.119	0.032	−0.19 to −0.06
Species	0.352	0.066	0.22–0.47

annual CWD ranged from 339.6 in 2011 (wettest year during the study period) to 832.1 mm yr^{−1} in 2014 (driest year during the study period), 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 by one year) following the onset of drought conditions in 2012.

Linear mixed-effect model results indicated that tree BAI (2008–2015) was associated with crown ratio, CWD (1-yr lag), competition, and species (Tables 2 and 3). Trees with higher crown ratios had higher BAI ($t = 3.25$, $P = 0.001$). Climate water deficit (1-yr lag) had a negative effect on annual BAI ($t = -17.77$; $P < 0.001$; Table 2). In general, Douglas-fir had higher annual growth than ponderosa pine ($t = 5.34$; $P < 0.001$; Fig. 2) with the exception of persistent (3rd and

Table 4

Selection of linear mixed-effects model for drought resistance in the fourth consecutive year of drought (2015) for Douglas-fir and ponderosa pine including crown ratio (CR), 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
DBH, Comp, Species, Comp ²	7	443.6	0.0	0.32
DBH, Comp, Species	6	444.0	0.4	0.26
DBH, Comp, Species, Comp ² , Comp ³	8	444.9	1.3	0.17
CR, DBH, Ht, Comp, Species	8	445.2	1.6	0.14
CR, DBH, Comp, Species	7	446.0	2.4	0.10
CR, Comp, Species	6	450.2	6.6	0.01

4th consecutive) and severe 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 unit improved the final model (conditional $R^2 = 0.71$).

3.2. Drought resistance

In general, as drought conditions persisted, mean drought resistance declined in both treatments, while differences in drought resistance between treated and untreated stands increased (Fig. 3). In the severe drought years of 2014 and 2015 (drought years 3–4), we detected

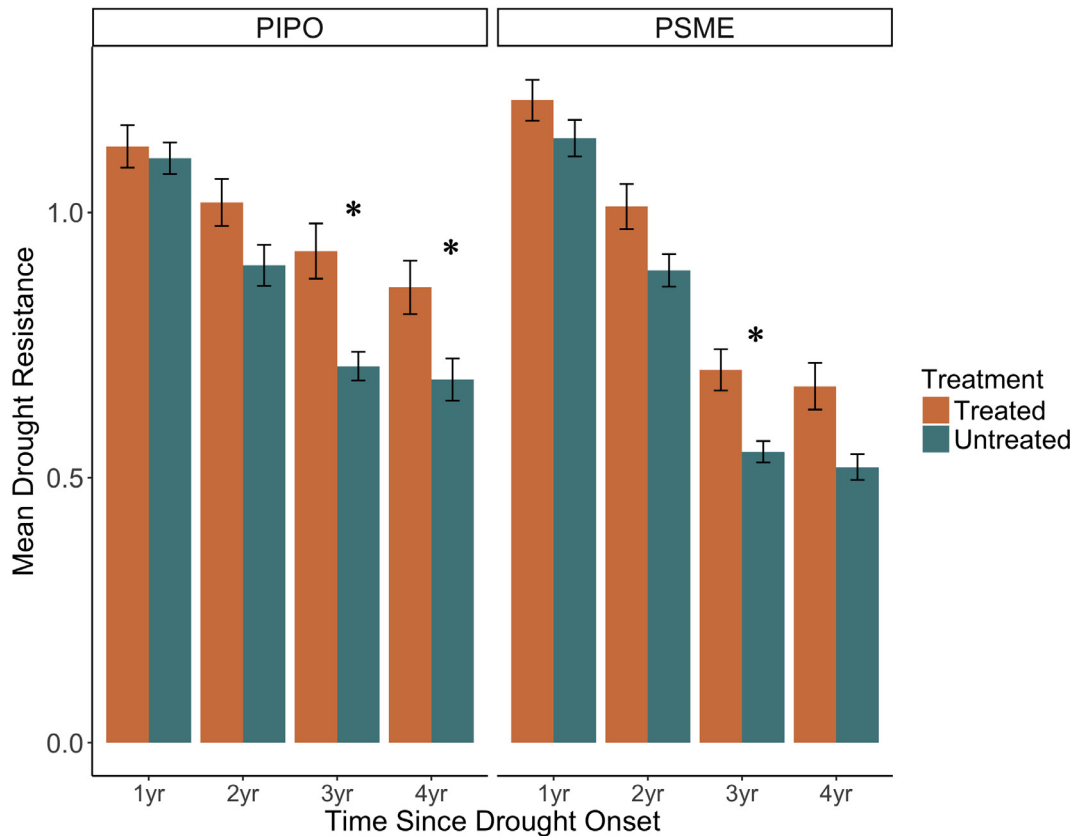


Fig. 3. Mean drought resistance by treatment for ponderosa pine (PIPO) and Douglas-fir (PSME) for several drought years beginning in 2012 (1 yr). Higher values of drought resistance represent less change in growth during drought relative to pre-drought conditions. Asterisks denote Tukey-adjusted significant species-level treatment differences ($\alpha = 0.05$) for drought year on the log-scale. Error bars represent standard error.

Table 5

Parameter estimates and variation for 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). Species differences are shown relative to ponderosa pine. Estimates are shown on the log-scale. Parameter 95% confidence intervals (CI) were estimated from 1000 bootstrapped samples.

Term	Estimate	Standard Error	95% CI
DBH	−0.01	0.002	−0.01 to −0.002
Comp	−0.06	0.021	−0.10 to −0.02
Species	−0.26	0.061	−0.39 to −0.14

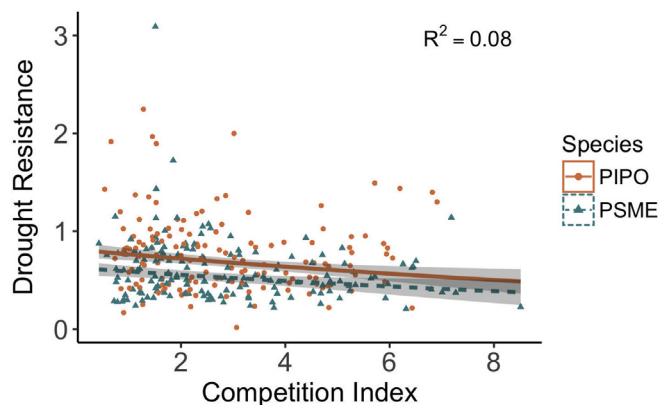


Fig. 4. Mean prediction lines for drought resistance across all units in the fourth consecutive year of drought (2015) in response to competition with standard error for ponderosa pine (PIPO) and Douglas-fir (PSME) from linear mixed-effects model. Scatter plot shows actual drought resistance values.

treatment-level effects for both 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: $F = 15.5$; $P < 0.001$) using an ANOVA. Median drought resistance during 2014 in treated stands 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 $P = 0.031$) compared to untreated stands (Fig. 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 higher but not quite significant for Douglas-fir ($df = 4$, t -ratio = -2.67 ; Tukey-adjusted $P = 0.056$).

Linear mixed-effects model results indicated that drought resistance during the severe and persistent drought year of 2015 (drought year 4) was negatively associated with DBH, competition, and species (Tables 4 and 5). Larger trees had lower drought resistance compared to smaller trees ($t = -2.72$; $P = 0.007$). Trees experiencing higher competition also had reduced drought resistance ($t = -2.81$; $P = 0.005$; Fig. 4). In general, Douglas-fir had lower drought resistance than ponderosa pine in the fourth year of drought ($t = -4.31$; $P < 0.001$). However, the inclusion of these factors in the final model explained a low amount of variability in drought resistance (marginal $R^2 = 0.08$), and the random intercept for unit only slightly improved the model (conditional $R^2 = 0.09$).

4. Discussion

4.1. 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 a more important predictor of annual 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 can increase crown ratio (e.g., Bailey and Tappeiner, 1998), which may improve growth during periods of climatic stress. Likewise, trees with less competition were growing faster on average than trees with more competition, a finding consistent with 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 tree-growth.

Analogous to other studies, we found that species-level growth responses to climatic stress varied and can have 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 water stress, however, these coping strategies can be ineffective, 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 thinning treatments (Fig. 2, Appendix A). Throughout most of the study period, Douglas-fir had higher BAI than ponderosa pine likely because Douglas-fir were generally younger. However, during the 3rd and 4th years of severe drought (2014 and 2015), annual growth of 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. For instance, Douglas-fir has greater leaf mass per area and greater photosynthetic capacity than ponderosa pine (Bond et al., 1999).

4.2. Drought resistance

Our results suggest that fuel reduction treatments may enhance drought resistance in mixed-conifer forests of WNRA, however, the effectiveness of treatments are dependent on factors such as drought persistence and tree characteristics. In general, these findings are consistent with other studies that found a positive effect of thinning treatments on growth inferred as a measure of drought resistance (Kohler et al., 2010, D'Amato et al., 2013, Bottero et al., in press). 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 and species). Similar to studies in the Sierra Nevada and southwestern US, we found DBH to be negatively associated with drought resistance, perhaps due to higher

water demand and/or greater leaf area for larger trees (D'Amato et al., 2013, McDowell and Allen, 2015). This result contrasts with findings that drought resistance was greater in larger diameter ponderosa pine (mean DBH 73.8 cm) in the southwestern US (Kerhoulas et al., 2013). Thus, tree and site characteristics are likely important in determining growth response to drought, but generalizations across a given species may not be appropriate.

Trees with less competition consistently demonstrated greater drought resistance during periods of severe climatic stress (also see Sánchez-Salguero et al., 2015). Reducing competition 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 can be less influential on growth during periods of heat and water stress (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 drier forest types (Allen et al., 2015). High levels of 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 unmeasured factors may be important in explaining variability in drought resistance.

Although drought resistance was improved in treated stands at WNRA during severe drought years, Douglas-fir may still be more vulnerable to the impact of drought than ponderosa pine. During the 3rd and 4th years of persistent and severe drought (2014 and 2015), Douglas-fir had lower mean resistance in treated and untreated stands compared to ponderosa pine. Increased drought sensitivity in Douglas-fir at our sites may be related to greater leaf area of the species generally (McDowell and Allen, 2015) and more variable growth patterns observed throughout the study period (Ogle et al., 2000, Fekedulegn et al., 2003; Appendix A). Other studies have linked low growth periods (Caillieret 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 BAI) at our study site. In persistent and severe drought years (2014–2015), ponderosa pine showed a significant positive response to thinning treatments, while Douglas-fir had a more varied response. Although ponderosa pine had lower drought sensitivity and a stronger response to treatments relative to Douglas-fir, in the face of climate uncertainty, it may be useful to manage for forest diversity (all native species) to bet hedge against varied responses to severe 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, our results were mixed. One explanation could be that fuel treatments at WNRA reduced 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 oak species). The benefits of thinning vary with intensity of treatment (e.g., Kohler et al., 2010, Kerhoulas et al., 2013, Bottero et al., in press, 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 untreated stands for ponderosa pine in the southwestern US. It is possible that more intensive thinning at WNRA would have resulted in more substantial growth benefits during the recent drought. Understanding the relationship between treatment intensity and growth response 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 five years since treatment. Potential growth benefits from the treatments were also likely limited by the poor growing conditions during the drought. In WNRA, mean treatment-level resistance declined in both treated and untreated stands throughout the 4-yr drought period, while the difference in resistance between the treated and untreated stands increased.

Another important dimension of drought response is resilience (Millar et al., 2007). Forest drought resilience is a measure of longer-term growth responses to drought events (Lloret et al., 2011). Since our samples were taken while California was still in a drought, evaluation of the subsequent recovery of forests from drought stress was not possible. Given the uncertainty in climate projections, monitoring and adaptively managing forest stand conditions may be the 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.

4.3. Conclusions

Overall, we found individual tree characteristics, local competition, and climatic stress to be important factors influencing tree-growth during the study period (2008–2015). Additionally, our results suggest that reducing stand density, and thus competition, can improve tree and treatment-level drought resistance during severe drought. However, these benefits are dependent upon tree characteristics, 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, managers could evaluate treatment effects and be prepared to adapt future prescriptions to changing conditions.

Declarations of interest

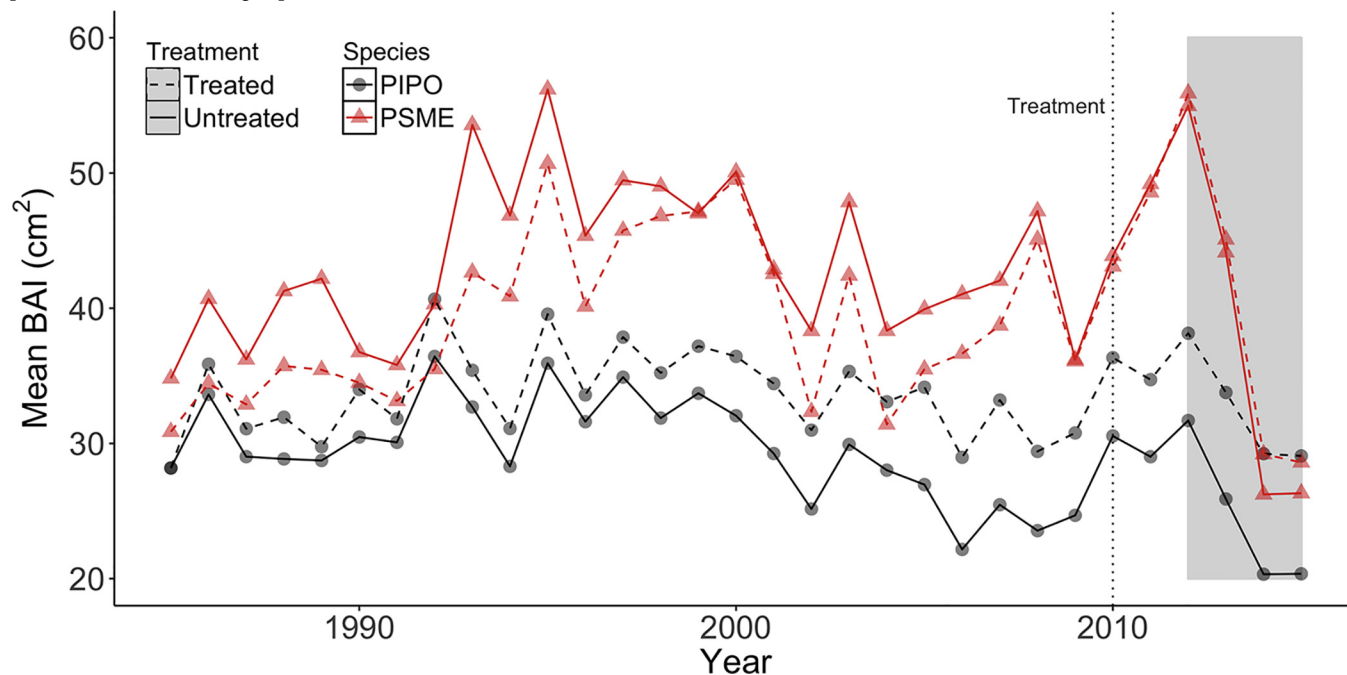
None.

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Appendix A

Thirty-year (1985–2015) mean growth trends for ponderosa pine (PIPO) and Douglas-fir (PSME) in treated and untreated stands. Gray box represents the recent drought period (2012–2015).



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