EFFECTS OF THINNING AND PRESCRIBED BURNING ON TREE RESISTANCE TO EXTREME DROUGHT IN A SIERRA NEVADA MIXED-CONIFER FOREST, CALIFORNIA USA.

By

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ABSTRACT

EFFECTS OF THINNING AND PRESCRIBED BURNING ON TREE RESISTANCE TO EXTREME DROUGHT IN A SIERRA NEVADA MIXED-CONIFER FOREST, CALIFORNIA USA.

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Drought-induced tree mortality can drastically alter forest composition, structure, carbon dynamics, and ecosystem function. Increasingly, forest policy and management focus on how to improve forest resistance and resilience to drought stress. This study used tree ring data at Teakettle Experimental Forest (TEF), a historically frequent fire mixed-conifer forest in the California Sierra Nevada, to quantify how prescribed fire and mechanical thinning conducted in 2001-2002 influenced stand and tree-level growth responses to the extreme California drought of 2012-2016. Overstory thinning and understory thinning significantly enhanced growth responses to treatments alone and treatments during the drought at the stand-level. In each year of the drought, distinct tree species were the only significant predictors of drought resistance at the stand-level. As drought persisted, shade-intolerant pine species yielded greater drought resistance values than shade-tolerant white fir and incense cedar. No prescribed burn effects were found, likely due low fire intensity. At the tree-level, tree diameter (DBH), tree height (HT), crown ratio (CRNR), topographic position index (TPI), and change in growing space over time (competition) were the most important predictors of growth responses to treatments and

drought resistance. Mechanical thinning, in both understory and overstory thinning can enhance mixed-conifer forests ability to resist drought by reducing competition and increasing resource availability. This study suggests forest managers have flexibility in prescribing various thinning intensities to promote drought resistance. Prescribed burn effects were not found in this study, but further research is needed to understand long-term burn effects for promoting drought resistance in Sierra Nevada mixed-conifer forests.

ACKNOWLEDGEMENTS

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INTRODUCTION

Climate projections suggest more frequent and severe drought events to occur globally, fundamentally altering forests in many regions (IPCC, 2007; Trenberth et al., 2014). Drought stress, associated water deficits and average warmer temperatures have recently been attributed to accelerated forest dieback internationally and throughout the western United States (Van Mantgem et al., 2009; Breshears et al., 2009; Allen et al., 2010; Anderegg et al., 2015). Drought disturbance in mixed-conifer forest ecosystems influences forest-growth dynamics such as tree vigor, productivity and survivable (Adams & Kolb, 2004; Kane, Kolb, & McMillin, 2014; Gazol et al., 2017). Drought-induced forest mortality alters forest structure, composition, and function, which can lead to undesirable forest conditions such as large contiguous stands of dead trees making forests exceedingly vulnerable to extreme fire behavior as dry fuel connectivity builds from the surface to crowns in dead trees (Clark et al., 2016). Severe drought events causing large-scale tree mortality may also reduce the quantity of merchantable timber; reduce carbon sequestration capacity due to ceased photosynthesizing of dead trees, and jeopardize the existence of wildlife habitat throughout the forest. Drought disturbance in mixed-conifer forests is naturally episodic; however, severe droughts causing excessive tree mortality pose potential undesirable outcomes to forest health and resources (North et al., 2012).

The recent and severe California drought from 2012 to 2016 substantially influenced mass forest mortality in the Sierra Nevada Mountains. This extreme drought had no disturbance-return period where the severe reduction in precipitation, snowpack duration, and soil moisture is without precedent in the instrumental record for California droughts historically (Robeson, 2015). The droughty climate conditions generated abnormally high winter minima temperatures, extremely low precipitation, and induced extensive forest mortality in the Sierra Nevada (Luo et al., 2017; Young et al., 2017). An estimated 102 million trees died in Sierra Nevada forests (Heath et al. 2016) during this drought due to synergistic effects of heightened competition, associated water stress, and endemic bark beetles (Goulden and Bales, 2019; Stephenson et al., 2019).

Forest densification catalyzed by 100 years of fire suppression in the Sierra Nevada exacerbated the effects of drought-stress on trees experiencing heightened competition for water (Larsson et al., 1983,Guarín and Taylor, 2005). Historical land management policies and practices excluding fire in the Sierra Nevada region altered the fire-adapted montane forests generally transitioning them into high-density stands composed of small-diameter, shade-tolerant trees (North, Innes, & Zald, 2008), thereby increasing fuel continuity and mass fire potential (Parsons and DeBenedetti, 1979; Stephens, 1998). The historical removal of fire in this landscape has proven to be disadvantageous during the drought. In 2012, at the onset of the California drought, these dense fire-suppressed forests were exceptionally stressed during droughty conditions with little water availability as trees in denser stands typically do not have adequate water resources in droughty conditions further predisposing them to pathogen or insect-induced mortality (Weed et al., 2013).

Under current projected climate scenarios, mixed-conifer forests are increasingly vulnerable to drought-induced mortality as greater demand for water is imposed by rising air temperatures (Williams et al., 2013). Trees in highly competitive environments likely have radial growth reductions, especially during drought, which suggests lower tree vigor and increased mortality risk (Cailleret et al., 2017). Using radial growth of trees, measured by annual rings in the wood, enables an understanding of tree vigor owing to the fact that tree rings serve as an integrative index for factors that limit tree growth-water, sunlight, nutrients, and competition for those resources. Therefore, trees that display increased annual radial growth increments suggests plentiful resource availability and a greater ability to resist disturbances, such as drought. To mitigate future drought-induced mortality, or increase resource availability, forest treatments such as prescribed fire and mechanical thinning can reduce competition for residual trees, increase radial growth increments, stabilize forest carbon, and enhance short-term drought resistance (Aussenac and Granier, 2008; Fecko et al., 2008; Hurteau and North, 2009, Van Mantgem et al., 2016a; Vernon et al., 2018). Using prescribed fire and mechanical thinning to improve growth rates of residual trees is well supported (Latham and Tappeiner, 2002; Busse et al., 2009; Hood et al., 2015). However, there is still uncertainty as to the longevity of treatment effectiveness, scales of treatment implementation, and what fire/thinning combinations are best to enhance drought resistance in mixed-conifer forests.

The patchy mosaic landscape of clumped trees and single trees that typify Sierra Nevada mixed-conifer forests suggests more emphasis towards stand- and tree-level analyses of forest treatment effects on drought resistance. Assessing different scales and combinations of prescribed fire and/or mechanical thinning results may clarify the efficacy of these treatments abilities to promote drought resistance by capturing the variation of individual tree responses that likely represent finer-scale microenvironment growing conditions better than stand-level averages of tree growth analyses do in the patchy forest mosaics throughout Sierra mixed-conifer forests.

In this study I examined how prescribed fire and mechanical thinning treatments applied in 2001-2002 in a California Sierra Nevada mixed-conifer forest effected residual tree growth at the stand-level and individual tree-level both after treatment and during the California drought of 2012-2016. Leveraging tree ring data, individual tree attributes, and topographic information I asked three key questions. First, what combination of thinning and prescribed burning treatments resulted in the greatest growth response, and was that growth response sustained (i.e. resistant) to extreme drought? Second, were stand-level (i.e. treatments) or individual tree attributes (species, size, competition, topography) more important drivers of tree growth response to the drought? Third, what specific tree attributes were associated with higher growth responses during drought?

MATERIALS AND METHODS

Study Site

The study was conducted at Teakettle Experimental Forest (TEF) approximately 80 km east of Fresno, CA in the Sierra National Forest. Elevation at TEF ranges from 1900 to 2600 m. Common soils are well-drained Dystric and Lithic Xeropsamments of loamy sand to sandy loam textures derived from granitic rock, while exposed granitic rock is common throughout the study area (USDA Forest Service and Soil Conservation Service 1993). The climate at TEF is Mediterranean, with hot dry summers and cool wet winters, and annual precipitation of 125 cm falls almost entirely as snow between November and April (North et al. 2002). The mixed-conifer forest at TEF is dominated by white fir (<u>Abies concolor</u> (Gord. & Glend.) Lindl. Ex Hildebr.), incense-cedar (<u>Calocedrus decurrens</u> (Torr.) Florin), sugar pine (<u>Pinus lambertiana</u> Dougl.) and Jeffrey pine (<u>Pinus jeffreyi</u> Grev. & Balf). Red fir (<u>Abies magnifica</u> A. Murr.), California black oak (<u>Quercus kelloggi</u> Newberry), and bitter cherry (<u>Prunus emarginata</u> (Dougl. ex Hook.) D. Dietr.) are also present. Hhistorically the mean fire return interval at TEF was 12–17 years, and the last major fire occurred in 1865 (North et al. 2005). Fire exclusion dramatically changed the forest composition and structure of TEF during the 20th century, reducing the proportion of large pines, increasing the density of smaller shade-tolerant white fir and incense-cedar, while also increasing the spatial clustering of trees at multiple spatial scales (North et al. 2007).

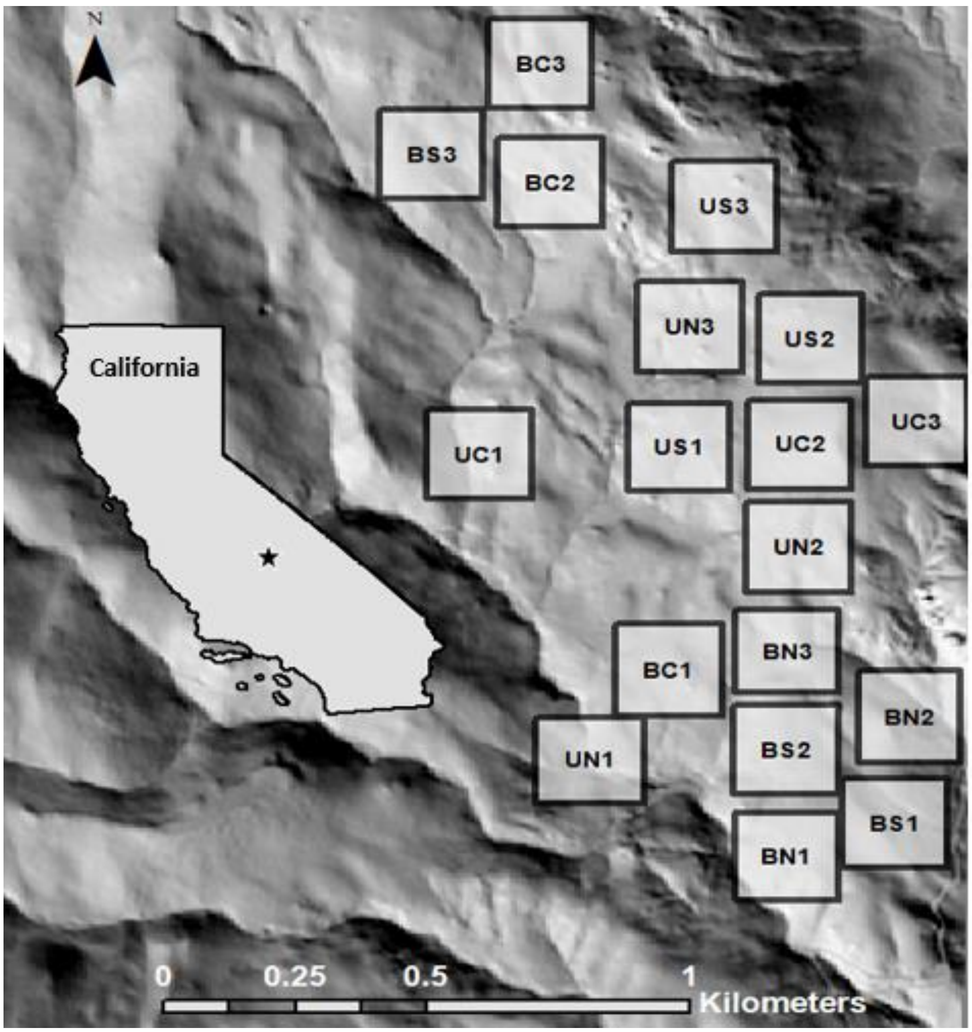

Figure 1. Locator map of Teakettle Experimental Forest (TEF) within California (indicated by black star). Plots outline overlain on a digital terrain model hillshade derived from aerial discrete return Light Detection and Ranging (LiDAR) data. Treatment unit outlines denoted as black squares. UN = unburned not thinned, UC = unburned with understory thin, US = unburned with overstory thin, BN = burned not thinned, BC = burned with understory thin, BS = burned with overstory thin. See methods for details regarding prescribed fire and thinning treatments.

Sampling Design

Experimental treatments at TEF were established as a full factorial restricted randomized design contrasting three levels of thinning and two levels of burning (Fig.1). The six treatments combinations were: unburned, no thin (UN) control; unburned, understory thin (UC); unburned, overstory thin (US); burned, no thin (BN); burned, understory thin (BC); and burned, overstory thin (BS). Understory thinning prescriptions followed guidelines in the California spotted owl (CASPO) report, removing trees 25-76 cm diameter at breast height (DBH, 1.37 m) while retaining at least 40% canopy cover (Verner et al., 1992). Initially designed to minimize impact to spotted owl habitat, the CASPO guidelines have been widely used for fuel management treatments (SNFPA, 2004). Overstory thinning (Shelterwood thin) removed trees >25 cm DBH, retaining approximately 22 regularly spaced large diameter trees (generally >100 cm DBH) per hectare. Overstory thinning (BS, US) was widely practiced on federal lands in Sierran forests before CASPO thinning treatments. Thin and burn treatments were thinned during the fall of 2000, and thin only treatments were thinned during summer 2001 using feller buncher machinery for tree harvests. Burning was applied in late October 2001, under fuel and fire weather conditions that resulted in a slow creeping ground fire with mean flame heights under 2 meters. Each treatment combination was applied to three 4 ha replicate plots, with treatment combinations assigned with restricted randomization because prescribed fire plots were clustered in three groups for fire operations containment concerns. All plots were individually lit under similar weather conditions.

However, prescribed burn treatments were ineffective at reducing basal area compared to the unburned treatments at TEF, where there was no significant difference in basal area between thin treatments and burn treatments (North et al., 2007). Post-treatment basal area in understory thin treatments was 41.2 (m^2/ha) and 37.5 (m^2/ha) in burn understory thin treatments. Post-treatment basal area in overstory thin treatments was 22.7 (m^2/ha) and 17.2 (m^2/ha) in burn overstory thin treatments. Post-treatment comparisons for unburned, no thin and burn, no thin also showed no significant difference in basal area with a change from 56.4 (m^2/ha) in the control to 53.7 (m^2/ha) in the burn, no thin treatment. There was significant differences in stand density (stems/ha) between thinning treatments with and without prescribed burns. Prior to treatment implementation (1998-2000, 2001-2002 for control plots) a complete census of all trees and snags > 5 cm DBH was conducted, trees and snags permanently tagged, identified to species, DBH measured, and mapped using a surveyor's total station. This census was remeasured in 2004, 2011, and 2017

Field Data Collection and Sample Processing

In summer 2017, tree cores were extracted and detailed individual tree measurements were collected at TEF using a stratified random design based on the permanent tagged stem map data collected in 2011. Only the four dominant trees species (A. concolor, C. decurrens, P. jefferyii, and P. lambertiana) were sampled. Sampling strata included these four species, the six treatment combinations, three DBH classes (10-25 cm, 25-55 cm, and > 55 cm), and two competition classes (high versus low competition). Competition was quantified by generating Thiessen polygons derived from the 2011 stem map of each plot at TEF. The Thiessen polygon area (m^2) around each tree was used as an individual tree metric of competition, with greater polygon areas suggest less competition (more growing space). Thiessen polygon areas greater than the median sized polygon per plot determined the "high" or "low" competition status for tree sampling. Previously at TEF, this Thiessen polygons have been successfully used as an individual tree competition metric to model past tree growth and growth-climate relationships (North et al. 2007, Hurteau et al. 2007). Tree lists by stratum were compiled, and trees sampled from a randomized list of tree tag numbers of trees satisfying the sampling combination criteria until five trees were sampled in each stratum. A total of 720 trees were sampled (4 species x 6 treatment combinations x 3 DBH classes x 2 competition classes x 5 trees per stratum). This resulted in a sample that represented the range of tree sizes and competitive environments across treatment combinations and species (Appendices 1-4). For each sampled tree, we collected two increment cores at breast height. For 432 of the sampled trees, both increment cores were collected using a 5 mm diameter increment borer, for the remaining 288 trees one of the two cores was collected using a 12 mm increment corer for a related stable carbon isotope study. For each tree, DBH, height, live crown ratio, and canopy class (dominant, co-dominant, intermediate, overtopped) were recorded. In the field, cores were taped onto wooden mounting sticks until they dried, and then were glued to the mounting sticks. Cores were sanded with progressively finer grit sand paper (up to 600 grit), and ring widths measured to the nearest 0.001 mm using either a flatbed scanner (minimum 600 dpi) with winDENDRO software (Regent Instruments, Quebec, Canada) or a stereozoom microscope with Velmex Unislide TA tree-ring measuring system (Velmexed, Bloomfield, New York). Tree ring series were cross-dated to ensure correct calendar year assignment of ring widths using the dplR package in R (Bunn et al., 2016). Cores that were damaged or otherwise unable to cross-date were discarded, resulting in cross-dated cores for 713 of the 740 trees sampled.

Topographic variables were generated from a digital elevation model (DEM) for Teakettle Experimental Forest derived from a large (approximately 20,000 hectare) lidar (light detection and ranging) data acquisition collected in 2010. Airborne discrete return lidar data was collected by Watershed Science, Inc. (Portland, Oregon, USA) on October 12-19, 2010 from a Cessna Caravan 208B fixed wing aircraft flown at 1100 - 1500 m above ground level. For the entire lidar acquisition, pulse return density averaged 8.8 points/m^2, and ground pulse density averaged 0.89 points/m^2. Root mean squared error between lidar points and 283 real time kinematic (RTK) GPS survey points was 0.004 m. From the lidar derived DEM, slope, cosine transformed aspect, and topographic position index (TPI) were calculated using the raster package in R (Hijmans, 2016). TPI is an index of elevation of a raster cell in relation to that of neighboring cells, and corresponds to position on the landscape. High TPI values represent ridgetops, and low values valleys and depressions. TPI was calculated at three neighbor spatial scales (10m, 50m, 300m). Average elevation, slope, aspect, and TPI values were extracted for coordinates of each mapped tree within a 10 m window.

Tree Growth Response and Resistance Metrics

Basal area increment (BAI) is an accurate measure of annual wood production. Annual BAI values were calculated from each ring width series and associated tree DBH values using the dplR package in R (Bunn et al. 2016). Additionally, the BAI calculations included a species-specific bark thickness equation for Sierra mixed-conifer species to each BAI measurement (Zeibig-Kichas et al., 2016) which provided stem wood BAI values excluding bark thickness. Series BAI values were then averaged for the paired cores to calculate annual BAI.

From the BAI values, three different growth response and resistance metrics were calculated for analyses focusing on growth response after treatments (R_{TRT}), growth response to treatments during the drought (R_{TRTD}), and growth resistance to the drought (R_D). The R_{TRT} variable was calculated as the average 2006-2011 BAI divided by the average pretreatment 1995-1999 BAI. The R_{TRTD} variable was calculated as the average drought (2012-2016) BAI divided by the average 1995-1999 BAI. The third response variable R_D was calculated as the average 2012-2016 BAI divided by the average 2006-2011 BAI, as described by (Lloret et al., 2011). These years (1995-1999, 2006-2011) of BAI growth were used because they avoided wetter than average years (NOAA) and years 2006-2011 were selected for post-treatment BAI measurements to avoid immediate post-treatment abnormalities in growth that can occur due to shock, mechanical damage, and fire damage (Harrington and Reukema, 1983; Agee and Skinner, 2005). These metrics enabled us to assess short-term treatment effects, if treatment effects were sustained during the drought, and if treatments were associated with changes in growth resistance to drought.

Statistical Analyses

We conducted all statistical analyses in R Version 3.5.2 (R Development Core Team, 2019). To evaluate treatment effects and species effects on tree growth response and resistance metrics at the stand-level we fit linear mixed effects (LME) models (713 focal trees) using the nlme package in R (Pinheiro et al., 2014). The models included three fixed effects (burn, thin, species) and all possible interactions among them. Individual treatment plots were included as a random effects term, due to unequal sampling of tree species in each replicate plot. Three different LME models with the same fixed effects, interaction terms, and random effects were developed to compare stand-level averages of growth response to treatments (R_{TRT}), growth response to treatments during the drought (R_{TRTD}), and growth resistance to the drought (R_D). Additional LME models for assessing growth response to treatments and drought resistance for each individual year of drought (2012-2016) were also included. Multiple comparisons tests using Tukey's adjustment compared levels of significant fixed and interaction effects in LME models.

To assess growth responses and drought resistance at the tree-level, we used Random Forest (RF) ensemble analysis to quantify the relative importance of each explanatory variable influencing tree growth and drought resistance for individual trees. This statistical method provided an improved variable selection process and enhanced our interpretive power for the final models. To assess relative importance and relationships between explanatory variables to tree growth responses and drought resistance, we used RF supervised machine learning algorithms with the randomForest package in R (Liaw and Wiener, 2002). In this study, RF selected 1,500 bootstrap samples, each containing two-thirds of the sampled cells. For each sample, RF generated a regression tree, then randomly selected only one-third of the predictor variables and chose the best partition from those variables.

Investigating tree-level characteristics and topographic environment variables influencing drought resistance, RF allowed us to quantify and evaluate relative importance of predictor variables determining growth responses and drought resistance to fire and/or mechanical thinning. In this study, significant explanatory variables included in the RF analysis were ranked and narrowed down to specific selection separately for each of the three models using the VSURF package in R (Genuer et al., 2015). Initially, VSURF ranked and selected from the complete list of individual-tree explanatory variables that included DBH, tree species, tree height, crown ratio, crown class, treatment, elevation, slope, transformed aspect (TASP), TPI, growing space, and competition (Thiessen polygon areas).

RESULTS

Stand-Level Responses to Treatments and Drought

The average growth trends of trees in thinning treatments showed a greater magnitude of increased and sustained growth post-treatment compared to growth trends of trees in non-thinned treatments (Fig. 2). Trees in thinning treatments (BC, UC, BS, US) also displayed sustained increases in growth during the drought compared to pre-treatment levels, meaning thinning effects sustained tree growth even during the drought.

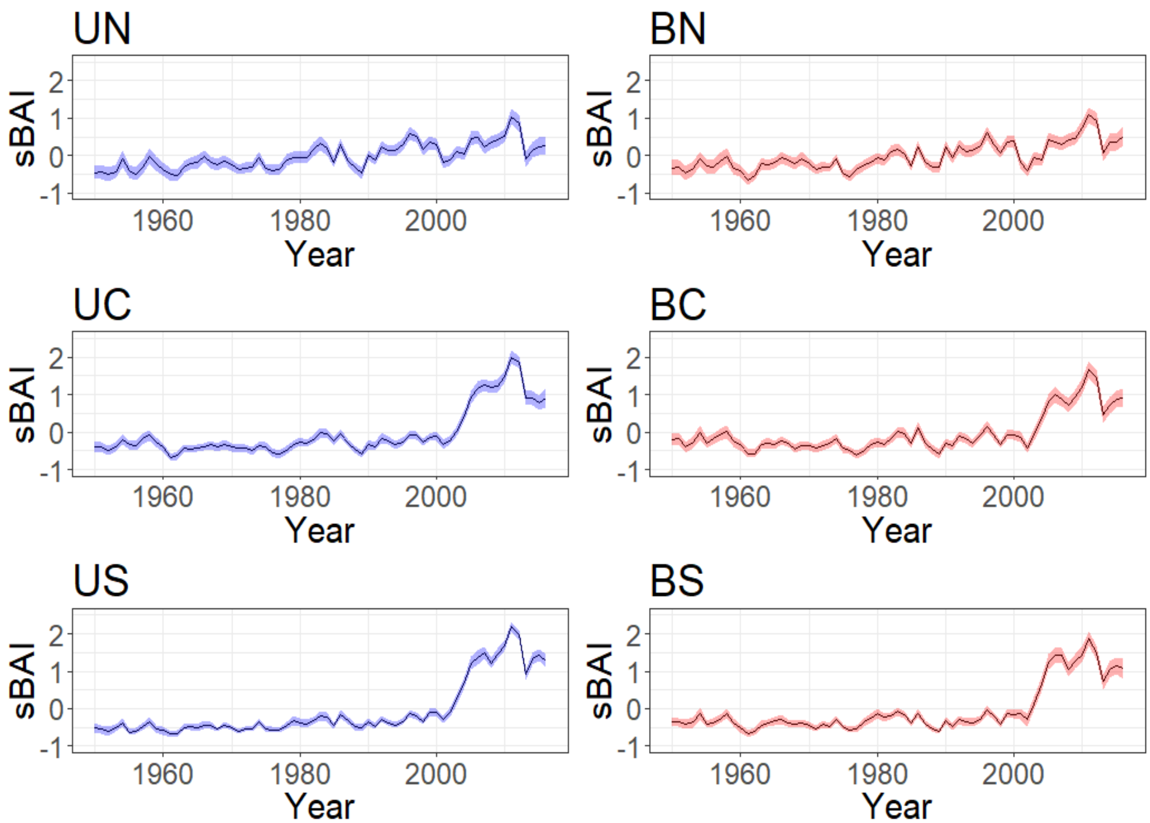

Figure 2. Average growth trends measured by standardized basal area increment (sBAI) for all trees in each treatment type during the last 66 years (1950-2016) at Teakettle Experimental Forest. Treatments implemented in 2000-2001. UN= unburned no thin, UC= unburned caspo (understory thin), US= unburned shelterwood (overstory thin), BN= burned no thin, BC= burned caspo (understory thin), BS= burned shelterwood (overstory thin).

Mechanical thinning, tree species and thinning: species interactions had significant effects on growth response to treatment (R_{TRT}) (Table 1). Only thinning treatments were a significant predictor of growth response to treatment during the drought (R_{TRTD}) (Table 2). However, no fixed or interactive terms were significant predictors for growth resistance to drought (R_D) at the stand level (Table 3). Furthermore, prescribed burn treatments had no significant effects on any of the three response metrics. Among all analyses in this study, there is no fixed burn effect (Table 1-3).

Table 1. ANOVA summary results from linear mixed effects model of growth response to treatment (R_{TRT}, 2006-2011/1995-1999) at the stand-level.

Model Parameters	**df**	***F*-value**	***p*-value**
BURN	12	2.9807	0.1099
THIN	12	34.5543	<0.0001
SPECIES	676	3.0702	0.0273
BURN:THIN	12	1.0709	0.3733
BURN:SPECIES	676	0.6343	0.5930
THIN:SPECIES	676	3.3408	0.0030
BURN:THIN:SPECIES	676	1.1255	0.3456

Table 2. ANOVA summary results from linear mixed effects model of growth response to treatment during the drought (R_{TRTD}, 2012-2016/1995-1999) at the stand-level.

Model Parameters	**df**	***F*-value**	***p*-value**
BURN	12	3.1473	0.1014
THIN	12	21.6253	0.0001
SPECIES	676	1.4592	0.2445
BURN:THIN	12	1.0530	0.3790
BURN:SPECIES	676	0.7134	0.5442
THIN:SPECIES	676	2.0020	0.0633
BURN:THIN:SPECIES	676	1.2767	0.2675

Table 3. ANOVA summary results from linear mixed effects model of drought resistance (R_D, 2012-2016/2006-2011) at the stand-level.

Model Parameters	**df**	***F*-value**	***p*-value**
BURN	12	0.0000	0.9985
THIN	12	0.1240	0.8844
SPECIES	676	0.9680	0.4072
BURN:THIN	12	0.3200	0.7321
BURN:SPECIES	676	1.1100	0.3441
THIN:SPECIES	676	0.2430	0.9621
BURN:THIN:SPECIES	676	0.5340	0.7827

Understory mechanical thinning treatments showed significantly greater average growth rates post-treatment compared to non-thinned stands growth post-treatment (2006-2011; t = 5.611; p= 0.0003; Fig. 3). Overstory thinning showed significantly greater average growth rates post-treatment compared to no thin stands growth post-treatment (2006-2011; t = -8.180; p = <0.0001; Fig. 3). However, there was no significant difference between overstory and understory thinning in growth responses to treatment (R_{TRT}) or treatments during drought (R_{TRTD}). Additionally, there was no difference among treatments for growth resistance to drought (R_D).

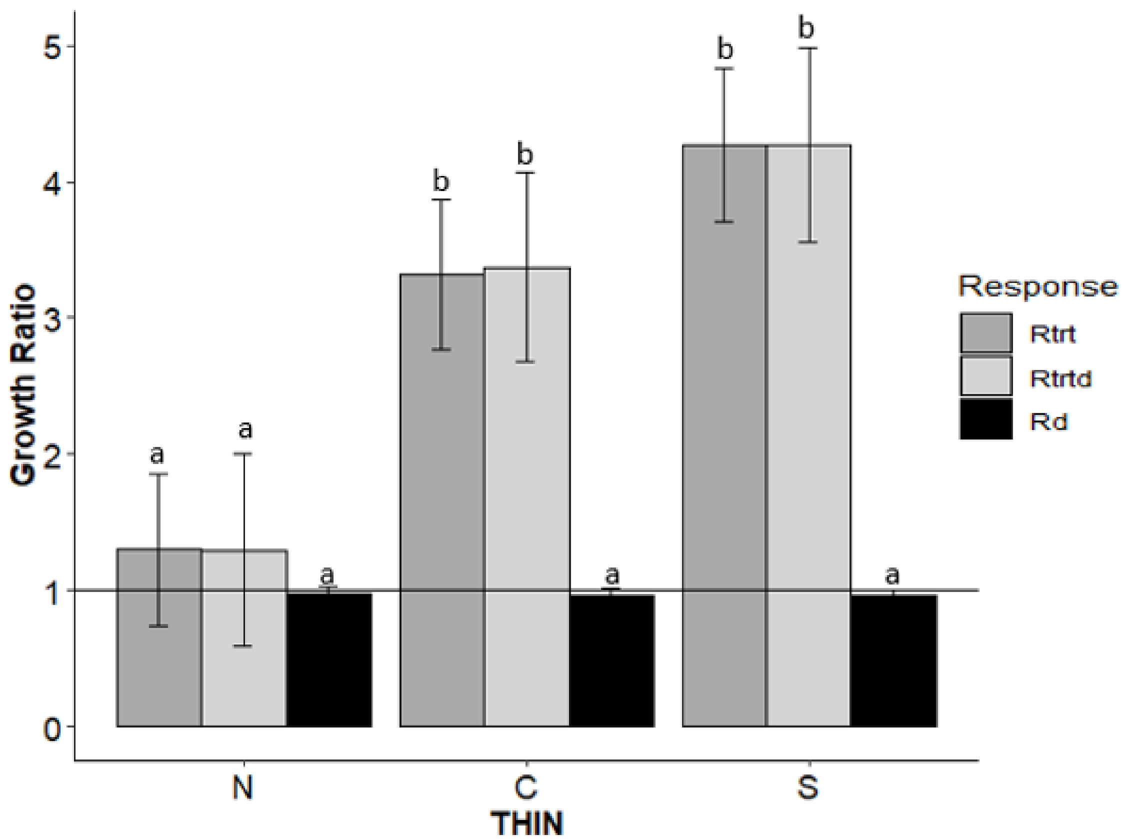

Figure 3. Comparisons of growth ratios (average basal area increments) by each response variable for all tree species and treatment types at Teakettle Experimental Forest. (N = no thin, C = caspo, S = shelterwood). The significance letters correspond to the associated differences for the same growth response, they do not correspond to the same thinning type, statistical comparison for identical colored bars. R_{TRT} = treatment response, R_{TRTD} = treatment response during drought, R_D = resistance to drought.

Among tree species, CADE (incense cedar) showed significantly greater average growth rates post-treatment than ABCO (white fir) growth post-treatment (2006-2011; t = -2.932; p= 0.018; Fig. 4).

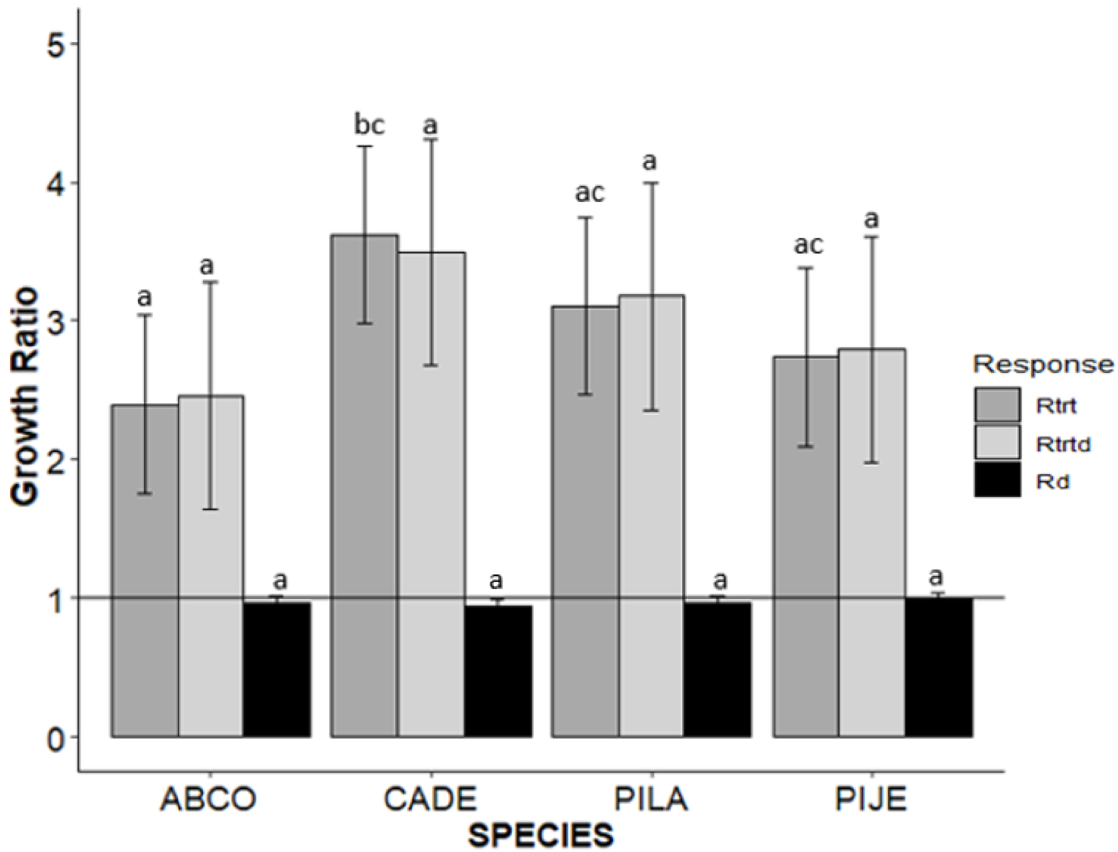

Figure 4. Comparisons of growth ratios (average basal area increments) by each response variable for (R_{TRT} = response to treatment, R_{TRTD} = response to treatment during drought, R_D = drought resistance) all tree species and treatment types at Teakettle Experimental Forest. Significance letters correspond to the associated differences for the same growth response, they do not correspond to same-species comparison, statistical comparison for identical colored bars.

Linear mixed-effects model post-hoc multiple comparison results indicate incense cedar in overstory thinning treatments demonstrated the greatest treatment growth response among all species and all treatment types (Fig. 5). Results show incense cedar has significantly greater treatment growth response than white fir in all treatment types from no thin, understory and overstory thinning treatments (df = 12, t = -6.845; Tukey-adjusted p= 0.0007; df = 12, t = -4.536; Tukey-adjusted p = 0.02; df = 676, t = -4.156; Tukey-adjusted p= 0.002; Fig. 5). Incense cedar also showed significantly greater treatment growth response than incense cedar in no thin treatments (df = 12, t = -6.904; Tukey's adjusted p= 0.0006; Fig. 5). Furthermore, incense cedar in overstory thinning treatments displayed significantly greater treatment growth response than sugar pine in no thin treatments and understory thinning treatments (df = 12, t = 6.656; Tukey-adjusted p= 0.0009; df = 12, t = 4.208; Tukey-adjusted p= 0.034; Fig. 5). Pairwise comparisons between thin: species interactions revealed significantly greater treatment growth responses in incense cedar than Jeffrey pine in no thin overstory thinning stands (df = 12, t = 6.345; Tukey-adjusted p = 0.001; df = 12, t = 4.485; Tukey-adjusted p= 0.0005: Fig. 5). Results indicated sugar pine in overstory thinning treatments demonstrates the second greatest treatment growth response among all species and all treatment types (Fig. 5). Post-hoc analysis results found sugar pine in overstory thinning treatments had significantly greater treatment growth responses than incense cedar in no thin stands (df = 12, t = -5.118; Tukey-adjusted p= 0.008; Fig. 5) and sugar pine in no thin stands (df = 12, t = -4.869; Tukey-adjusted p= 0.012; Fig. 5).

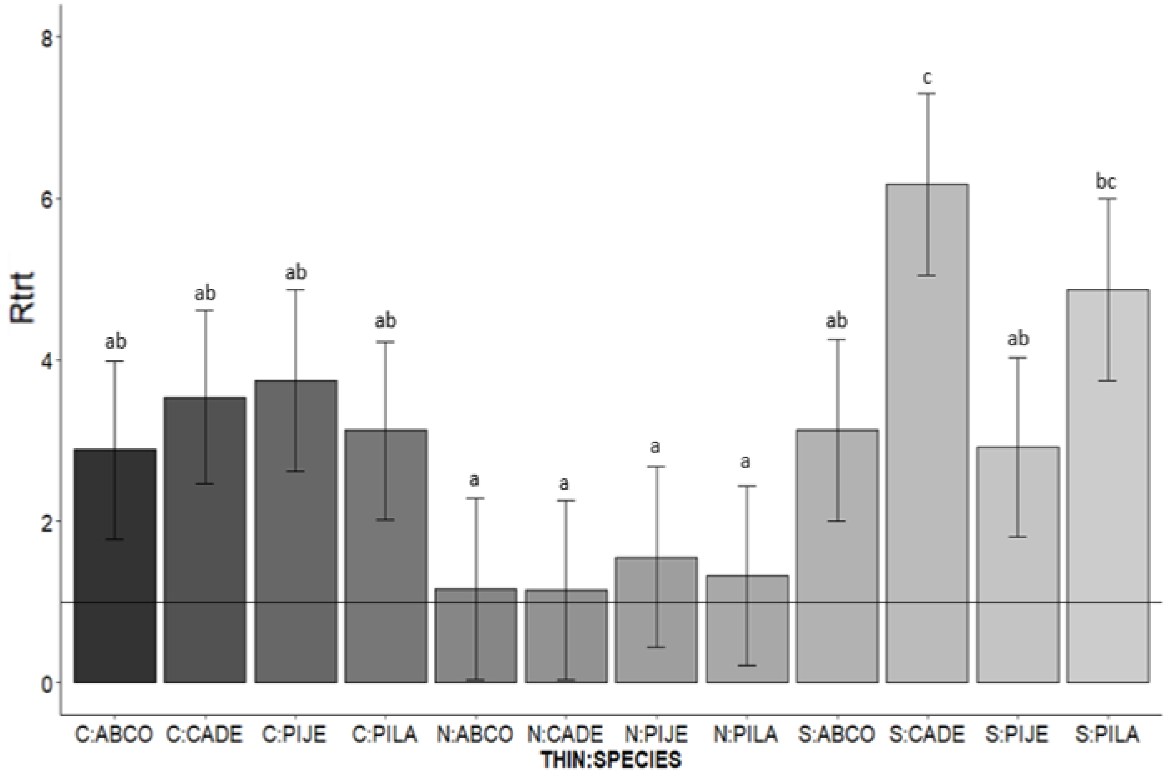

Figure 5. Treatment growth response values (R_{TRT}) for each thinning treatment: species interaction ordered by thinning treatment type, c = caspo (understory thin), n = no thin, s = shelterwood (overstory thin). Average growth response to treatment (R_{TRT}) (BAI) for each interaction at Teakettle Experimental Forest. Letters of significance represent results of differences between treatment growth responses by species and associated treatment, alpha = 0.05, similar letters indicate non-significance, statistical comparison for identical colored bars.

Tree species was the only significant predictor of drought resistance at the stand-level for each year of drought except in 2014 (2012, df = 676, *F*-value = 4.21; *p*= .005; 2013 df = 676, *F*-value = 3.27; *p*= .02; 2015, df = 676, *F*-value = 5.77; *p*= .0007; 2016, df = 676, *F*-value = 8.55; *p*= <.0001). There was no clear pattern among species influence on drought resistance in each year of the drought. Multiple comparisons show several variations of significant differences in species drought resistance for each year of drought (Fig. 6).

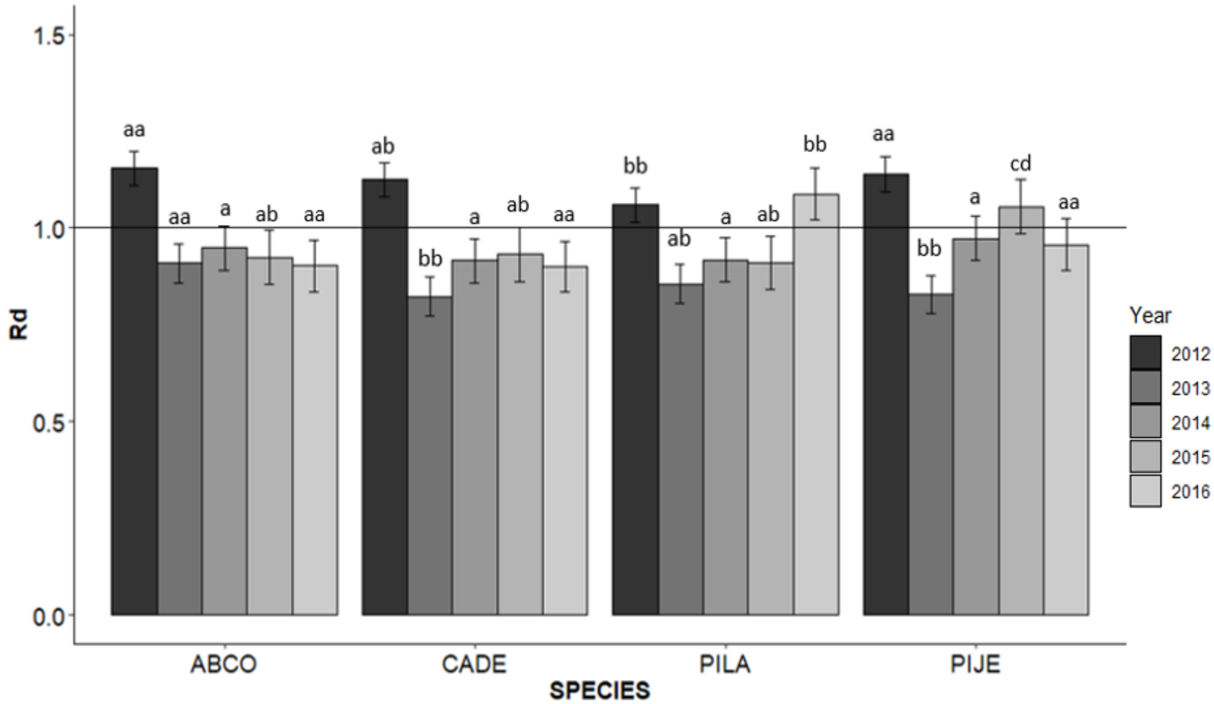

Figure 6. Drought resistance for each species ABCO = white fir, CADE = incense cedar, PILA = sugar pine, PIJE = Jeffrey pine. Displaying average drought resistance values in each drought year ("R_D") for all sampled trees at Teakettle Experimental Forest. Letters of significance represent results of differences between each drought year for differences in drought resistance, alpha = 0.05, similar letters indicate non-significance.

Mechanical thinning was a significant predictor of growth responses to treatment during each year of drought (R_{TRTD}) for the entire drought at the stand-level (2012, df = 12, *F*-value = 21.68; *p*= <.0001; 2013, df = 12, *F*-value= 21.25; *p*= 0.0001; 2014, df = 12, *F*-value= 21.06; *p*=0.0001; 2015, df = 12, *F*-value= 23.13; *p*= 0.0001; 216, df = 12, *F*-value= 18.38; *p*= 0.0002). Both overstory thin and understory thin were significant predictors of growth responses to treatment during the drought, however, there was no significant differences between the overstory and understory thin effects (Fig.7).

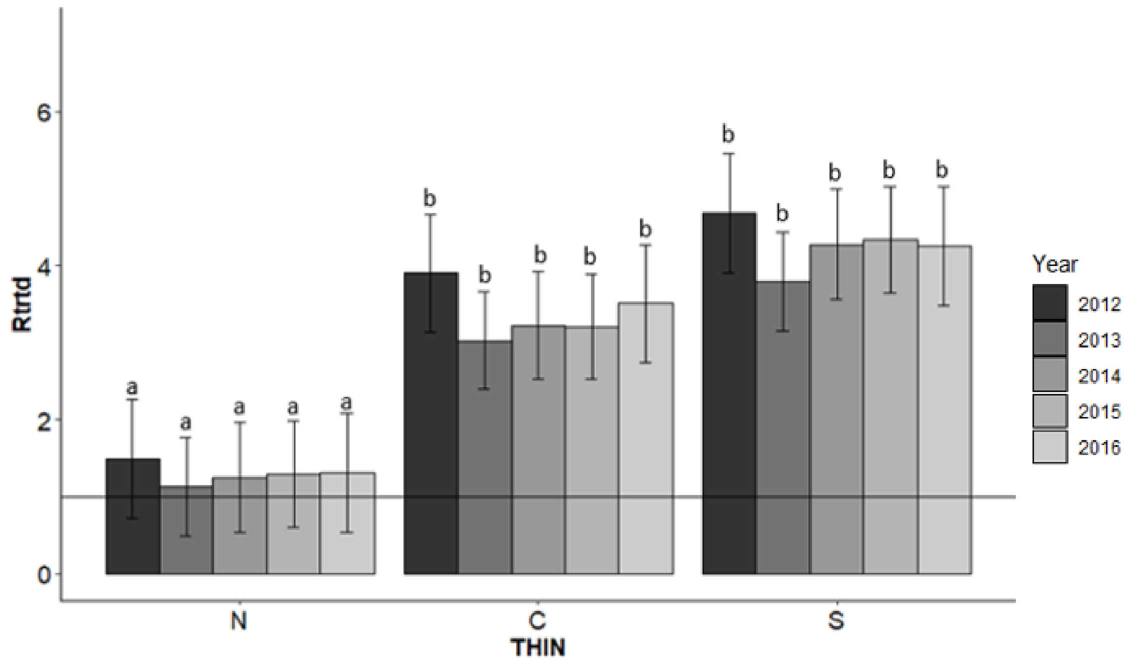

Figure 7. Treatment growth response for each thinning treatment ordered by thinning type n = no thin, c = caspo (understory thin), s = shelterwood (overstory thin). Displaying growth responses to treatment in each drought year (R_{TRTD}) for all sampled trees at Teakettle Experimental Forest. Letters of significance represent results of differences between each drought year for treatment growth, similar letters indicate non-significance.

Tree-level Responses to Treatment and Drought

A two-stage variable selection process retained four and five predictor variables in the final RF models that analyzed treatment growth responses during drought (R_{TRT}, R_{TRTD}) (Fig. 8) and five predictor variables in the final RF model that analyzed drought resistance (Fig. 8). For RF models, tree diameter (DBH) was the most important predictor of tree-level growth response to treatment and growth resistance to drought (Fig. 8) while change in growing space area (m^2) from 2001-2011 (pre-treatment to 2011) was the second most important predictor variable in determining treatment and drought growth response (Fig. 8). Across the entire study DBH was the strongest predictor variable overall in determining tree growth responses to disturbances and tree drought resistance (increasing MSE by 22.3% for treatment growth response, increasing MSE by 12.2% for drought growth response, increasing MSE by 39.6% for overall tree drought resistance, Fig.8). Difference in growing space area (m^2) from 2002-2011 (pre-treatment to 2011) was the second most important predictor variable in determining tree growth response to treatments (17.1%) and during drought (10.5%). Tree height (HT) was the second most important predictor variable in determining individual tree drought resistance (26.1%). Other predictor variables also showed significant importance in tree growth responses to treatment and drought (Fig.8). Change in growing space due to treatment was the next most important predictor in RF models explaining growth responses (17.1% for treatment response and 10.5% for drought response). The final important predictor for growth responses was treatment types 10.2% for treatment response and 10.5% for drought response). The next significantly important predictor in determining drought resistance after tree height and diameter was the crown ratio (18.5%), followed in rank by TPI at 300-meter resolution (14.9%), growing space pre-treatment (10.4%), tree species (7.1%), and difference in growing space area (3.9%) (Fig. 8).

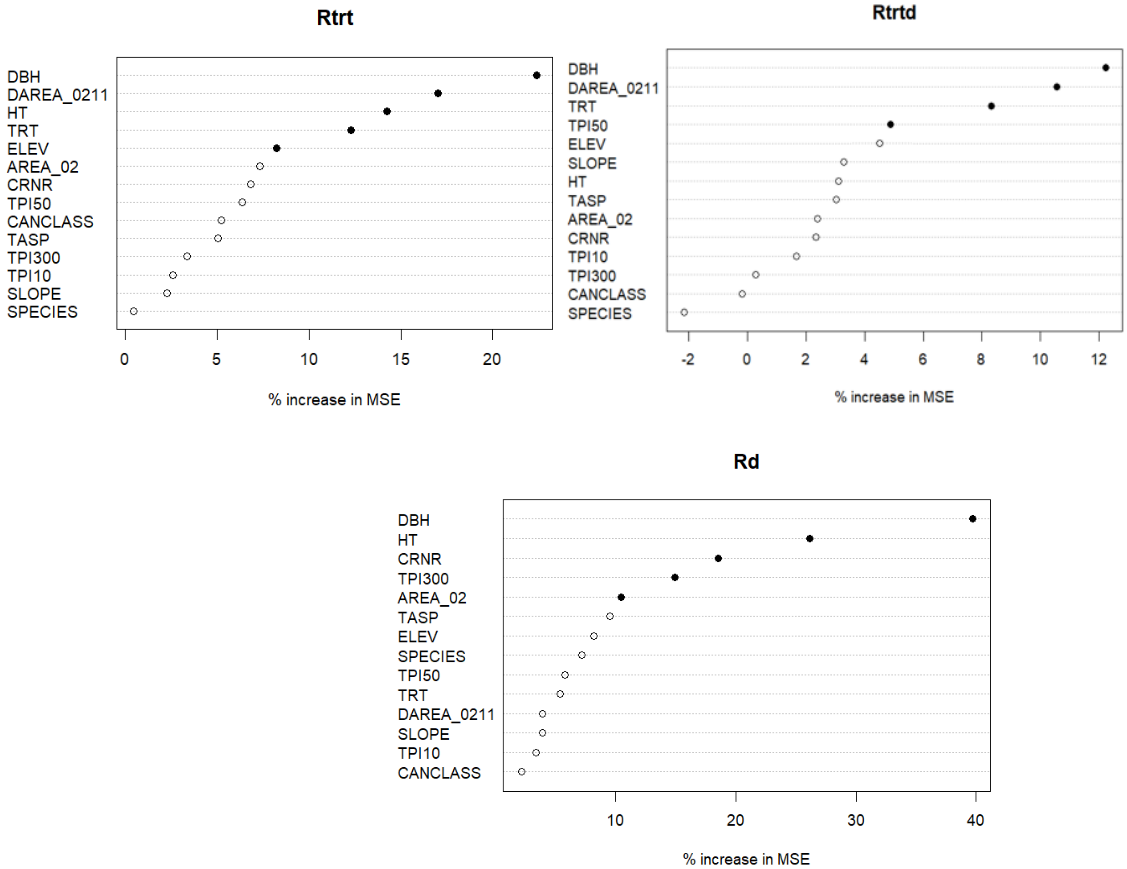

Figure 8. Variable importance plots from Random Forest (RF) models of tree-level growth responses to treatment (R_{TRT}), growth responses to treatment during drought (R_{TRTD}), and drought resistance (R_D) for each predictor variable including all sampled trees at Teakettle Experimental Forest. Solid circles denote variables retained in two-stage variable selection; open circles denote variables removed from the final RF models during variable selection. DAREA_0211, difference in growing space area (m^2) 2002-2011 (pre-treatment to post-treatment), AREA_02, growing space area (m^2) pre-treatment, CRNR, tree crown ratio, TPI, topographic position index at 10- 50- 300-meter resolutions, TASP, transformed aspect, MSE, Mean Squared Error.

The predictor variable "DAREA_0211" in the RF analysis represented the change in growing space (m^2), a representation of competition for each individual tree from pre-treatment (2000) to post-treatment (2011), there was simply a naming issue due to stem map modifications made in 2002 for the data collected in the summer of 2000 at TEF. A result of descriptive statistics among the average change in growing space for each treatment from 2000 (pre-treatment) to 2011 (post treatment) illustrates the variation of growing space changes by treatment that individual trees were sampled from (Fig. 9).

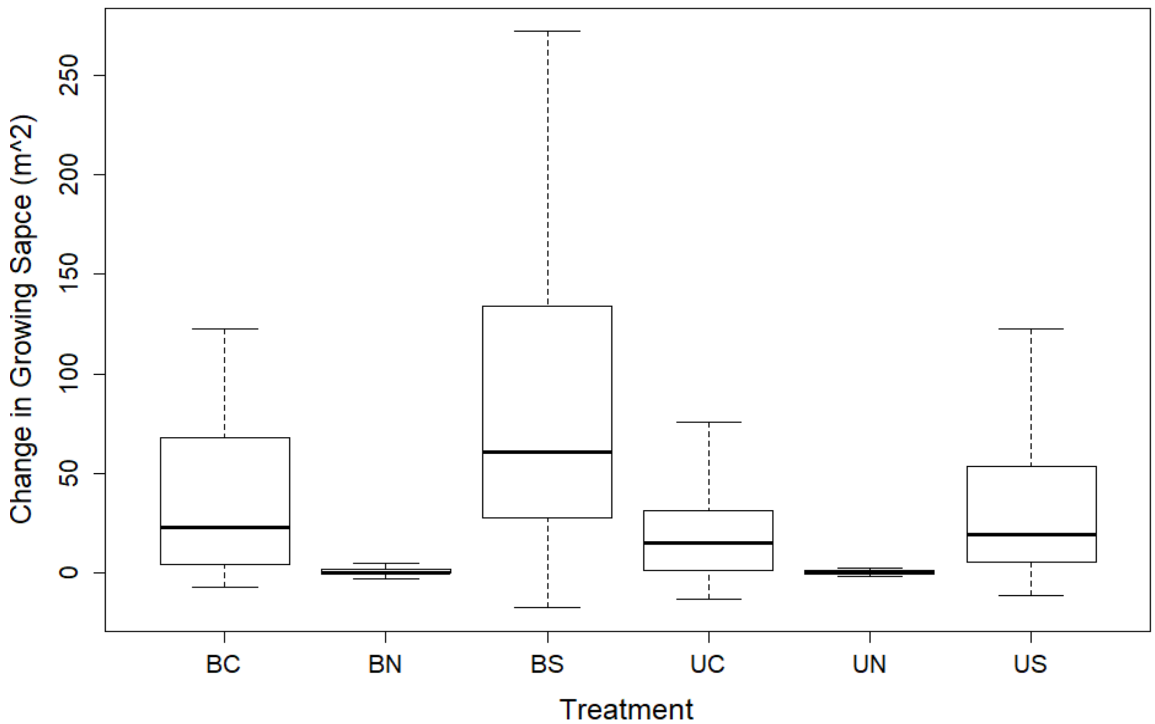

Figure 9. The average change in growing space for each tree from pre-treatment (2000) to post-treatment (2011) in all six treatment types at Teakettle Experimental Forest. UN= unburned no thin, UC= unburned caspo (understory thin), US= unburned shelterwood (overstory thin), BN= burned no thin, BC= burned caspo (understory thin), BS= burned shelterwood (overstory thin).

Partial dependency plots of RF models visualize a few key relationships between growth response metrics, drought resistance and predictor variables (Figs. 10,11,12), Tree growth responses decreased with larger DBH trees and increased with greater change in growing space from pre-treatment to post-treatment (Fig.10,11).

Growth responses to treatment and drought were generally higher in medium size-class trees and trees with greater change in growing space from pre-treatment to post-treatment. Although, growth responses and drought resistance declined exponentially with increasing DBH (Figs. 10,11,12). US plots showed the greatest R_{TRT} values among all treatment types (Fig. 10). Tree height showed a slightly negative relationship with growth responses to treatment and elevation lacks any obvious relationship with R_{TRT} values (Fig. 10).

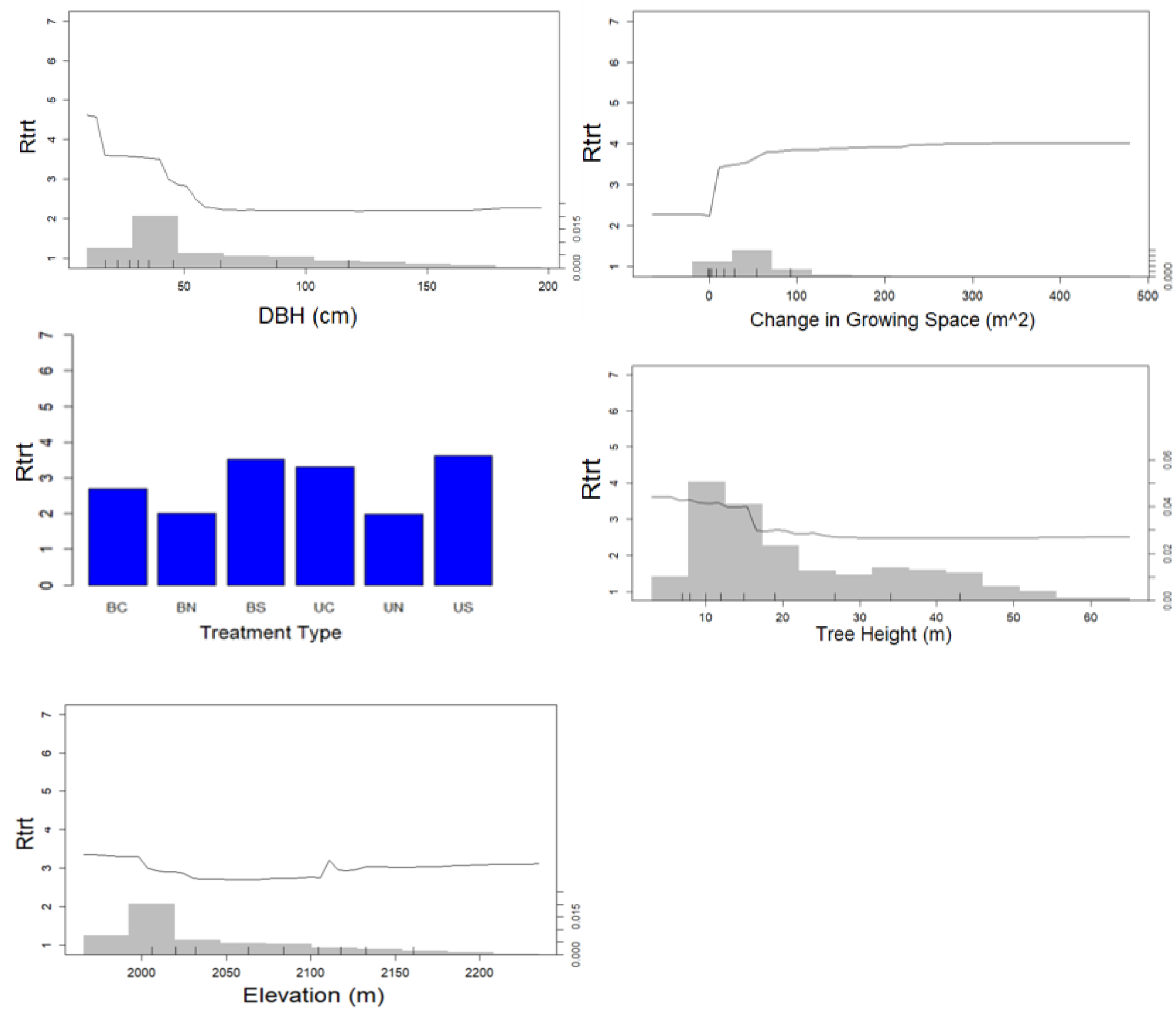

Figure 10. Partial dependency plots showing relationships between the most important predictor variables influencing treatment growth responses (R_{TRT}), DBH (centimeters), change in growing space from pre-treatment 2001 to post-treatment 2011, treatment types, tree height (meters), and elevation (meters) in random forest models. Solid lines show trends in treatment growth responses, underlain histograms show the distributions of data for each predictor variable.

Treatment type was a significant predictor of growth response to treatment during drought at the tree-level, where US plots had the greatest R_{TRTD} values among all treatment types (Fig. 11). TPI (50 m) showed no clear relationship with growth responses to treatment during drought but was a significant predictor (Fig. 11).

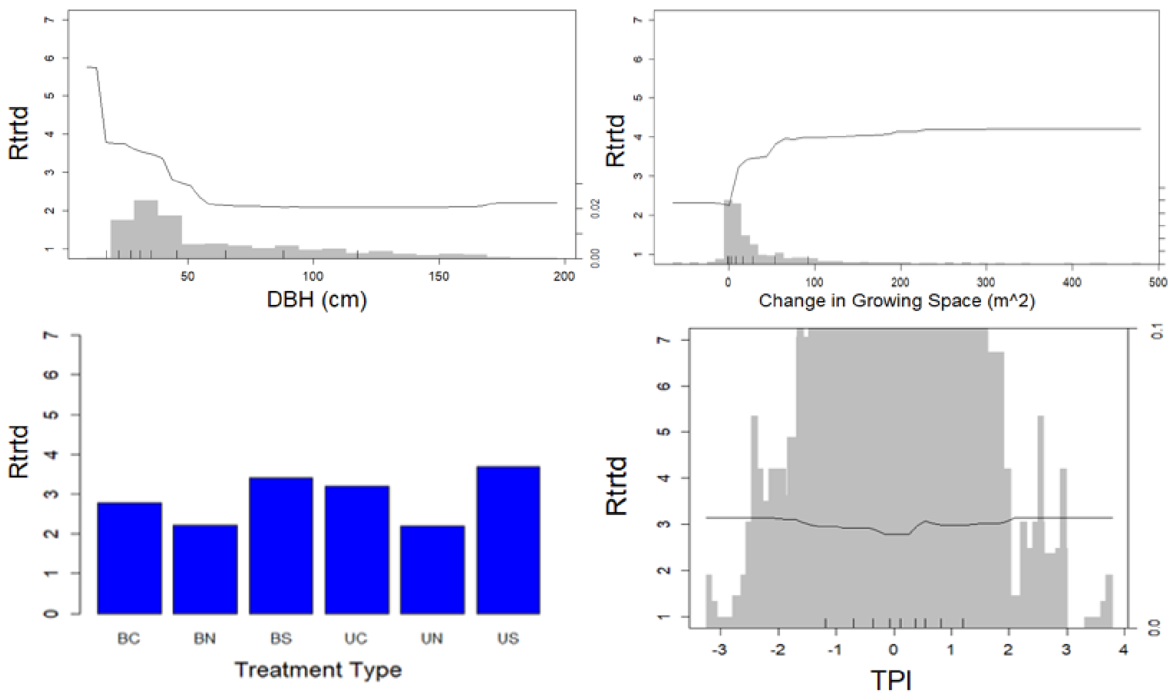

Figure 11. Partial dependency plots showing relationships between the most important predictor variables influencing treatment growth responses during drought (R_{TRTD}), DBH (centimeters), change in growing space from pre-treatment 2001 to post-treatment 2011, treatment type, TPI topographic position index (50 meter resolution), and elevation (meters) in random forest models. Solid lines show trends in treatment growth responses, underlain histograms show the distributions of data for each predictor variable.

Drought resistance values trend downward with increasing DBH, suggesting smaller to medium diameter trees demonstrate greater drought resistance than larger trees (Fig. 12). Among other included predictor variables in the final RF model, drought resistance showed no clear relationships with significant predictors.

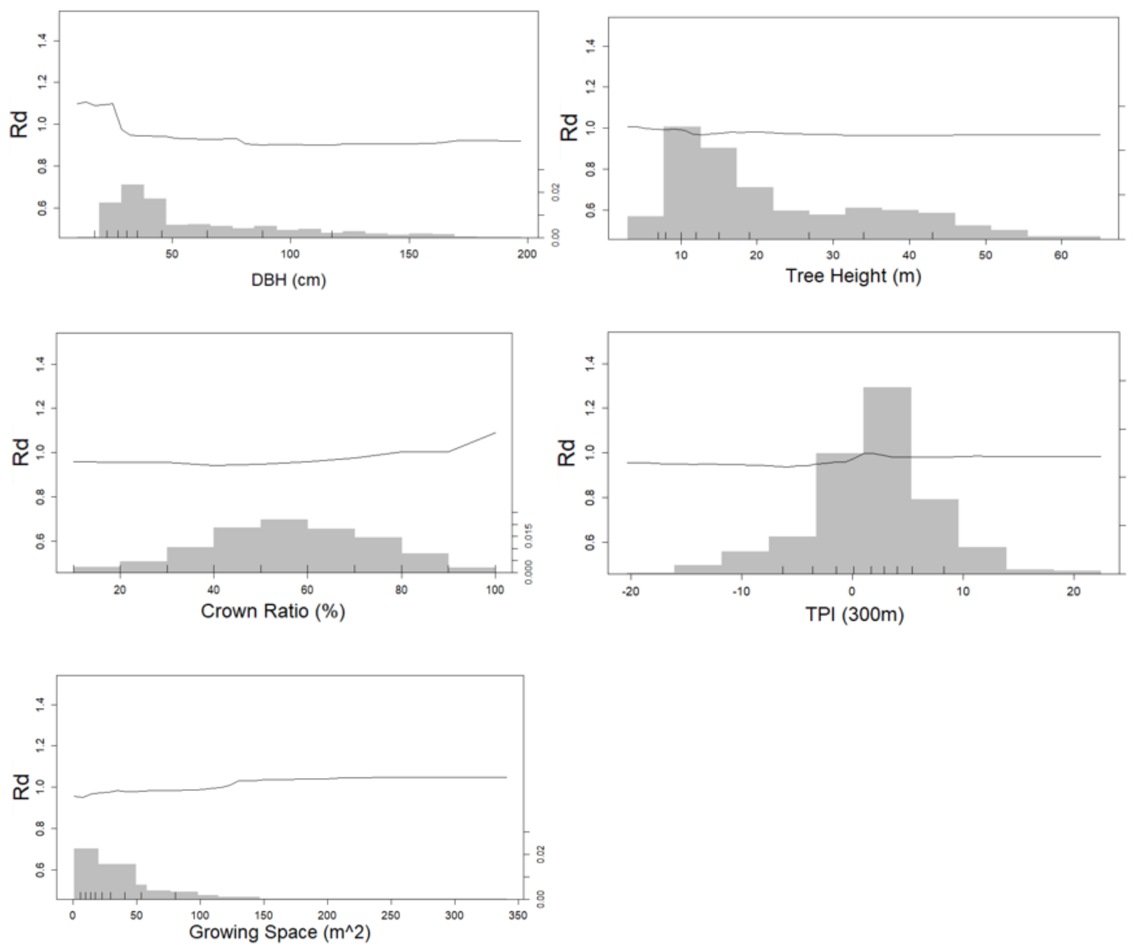

Figure 12. Partial dependency plots showing relationships between the most important predictor variables influencing drought resistance (R_D), DBH (centimeters), tree height (meters), crown ratio, TPI topographic position index (300-meter resolution), growing space pre-treatment (pre-2002), in random forest models. Solid lines show trends in drought resistance values, underlain histograms show the distributions of data for each predictor variable.

DISCUSSION

Quantifying forest drought resistance from tree rings elucidated effects of forest management treatments on stand-level and tree-level growth responses in a mixed-conifer forest. This study aimed to improve the understanding of mechanical thinning and prescribed burning treatments ability to promote drought resistance in a Sierra Nevada mixed-conifer forest, California USA. At Teakettle Experimental Forest, overstory and understory thinning showed the capability to improve BAI of all residual trees even during drought conditions. Prescribed burning, in this experiment, failed to promote significant growth responses or drought resistance. Species is an important variable in determining drought resistance as drought conditions persist. Below I discuss different variables that influence tree growth and drought resistance, and why stand- and tree-level distinctions are important. I will further discuss why burning treatments failed to promote growth and drought resistance as well as the possible management implications these findings pose for mixed-conifer forests in the Sierra Nevada.

It is important to note trees sampled for growth rates in this study were all still alive after surviving the California drought (2012-2016). Therefore, growth responses and drought resistance findings are conditional on the premise that only live trees were cored and measured.

At the stand-level, both understory and overstory thinning had comparable growth responses sustained during the drought and these responses were improved relative to un-thinned stands, indicating overstory or understory thinning is a viable option to enhance sustained radial growth and likely promote long-term drought resistance. The understory thin removed all trees between 25-55 cm DBH, and the overstory thin removed all trees >25cm DBH except 22 large (>76cm) DBH trees which suggests a strict diameter limits in harvesting prescriptions are not necessary to promote residual tree growth. The large differences in thinning intensity measured by post-treatment stand density, basal area, and canopy cover between understory thin and overstory thin treatments (North et al. 2007), suggests a wide range of treatment intensity can effectively promote sustained growth even during droughty conditions. The obvious differences in growth responses of mechanical thinning treatments compared to non-treated stands supports a well-understood effect of competition release from thinning disturbances (Mitchell et al., 1983; Vernon et al., 2018).

The lack of burn effects is likely due to the low intensity of the 2001 prescribed fires that failed to kill enough trees to significantly reduce competition. Fuel moisture levels at time of fire implementation were elevated due to precipitation that occurred the day before burning began, and an early winter storm resulted in snowfall one week after the burn. These moisture conditions moderated likely moderated fire intensity and effects. Post-fire treatment stand conditions showed no significant differences in basal area (m^2/ha) compared to thin-only stands (North et al., 2007). This contrasts other studies that found prescribed fire to significantly reduce basal area and stem density in Sierra mixed-conifer forests (van Mantgem et al., 2011). Additionally, 15 years after treatments, shrub cover (mountain whitethorn (C. cordulatus) and greenleaf manzanita (A. patula) was 98% higher in burn overstory treatments, and 55% in burn understory treatments (Goodwin et al., 2018). This large increase in shrub cover may have negated the potential burn effects in promoting growth responses and drought resistance in this study as competition for water increases with proliferating shrub regeneration in Sierra mixed-conifer forests (Royce and Barbour, 2001). In combination, the effects understory, overstory thinning, and prescribed burning make indicate that varying levels of competition reduction have comparable effects of tree growth response and drought resistance, but the negative effects of increased shrub competition, increased evaporative demand, and increased canopy vapor pressure deficit in overstory thinned and burned treatments may be obscured in this study. This suggests further research is needed on the effects of shrub competition and thresholds of competition reduction and how the may impact tree growth and drought resistance. Perhaps, prescribing more aggressive and more frequent burning in fire-suppressed mixed-conifer forests after thinning would consume the initial sprouting of shrub species and generate desirable competition reduction to promote greater growth responses and drought resistance in residual conifers.

Species effects varied by each individual drought year for drought resistance and was the only significant predictor of drought resistance at the stand-level. All species declined in growth after the first year of drought (2012), however, a general trend emerged; shade-tolerant tree species (white fir and incense cedar) grew at a reduced rate consistently during the entire drought duration (2012-2016), counter to this, both shade-intolerant species (Jeffrey pine and sugar pine) improved and demonstrated greater growth responses as drought persisted (2015-2016). The pine species were able to improve and sustain BAI growth during the drought as some studies have shown Jeffrey pine accessing deeper water sources through bedrock substrate (Rose et al., 2003), which could explain greater drought resistance in the Jeffrey pine and sugar pine species later in the drought due to unique bedrock water availability. Other studies found multi-year deep soil drying to strongly predict tree mortality, perhaps the pine species began to thrive after surrounding more shallow rooted species died-off and released water resources to the residual deeper-rooted pine species (Goulden and Bales, 2019).

From RF models, variable importance values show individual tree attributes are more important predictors of growth than stand-level treatment combinations. Tree diameter (DBH) was the most important predictor among growth responses and drought resistance. Tree height was also an important predictor of growth responses and drought resistance. The heterogeneous soil matrix typical of Sierra mixed-conifer forests plays a crucial role in developing a patchy mosaic landscape mixed by high-density clumps of trees, gaps, and individual stems where soil thickness and type strongly influence productivity (Meyer et al., 2007). Individual-tree analysis likely provided a better representation of the minute differences in singular tree microenvironments compared to broader stand-level averaging analysis.

At the individual tree-level, larger diameter trees showed lower growth responses and were less drought resistant overall. This is a concerning finding, as large trees are important for seed sources, wildlife habitat, and carbon stability, among many other forest attributes (Lutz et al., 2012; North et al., 2009). The result that larger diameter trees are the least responsive to treatments is crucial information for forest managers and policy makers. Why are the largest trees at TEF performing poorly? Studies have shown that larger diameter trees allocate more carbon reserves to resin ducts than trees killed during drought and insect-outbreaks (Kane and Kolb, 2010). The fact that only live trees were sampled for this study suggests these larger trees may have survived the California drought due to carbon allocation for radial growth to support resin duct production and increase defense against bark beetles. It is also important to note that the growth metrics used in this study are growth ratios, and so they make not reflect other metrics of performance (such as volume growth and carbon sequestration) that will be greater for larger versus smaller trees with the same values of ratio based growth response and resistance metrics.

At Teakettle Experimental Forest, mechanical thinning was successful in promoting residual tree growth while prescribed burn effects were negligible. Tree growth promoted by thinning treatments was sustained and likely makes these trees better adapted for long-term drought conditions. Tree species was the only significant predictor of the formal drought resistance metric, where both the Jeffrey pine and sugar pine species improved growth after the first year of drought, inspiring those restoration efforts trying to bring pine species composition back to the majority in Sierra Nevada mixed-conifer forests. Returning Sierra mixed-conifer forests back to frequent-fire ecosystems is agreeable in the long-term; our results showed no burn effects in promoting drought resistance but after more than one-hundred years without the presence of a fire at TEF it will presumably take more than just one prescribed fire to restore the natural historical benefits. Mechanical thinning provided a rapid residual tree growth response and served as a surrogate for high-severity fires by removing a large magnitude of stems in thin treatments (Knapp et al., 2017), however, in the long-term prescribed fire should be implemented continuously to maintain the historical fire-regime of Sierra Nevada mixed-conifer forests prior to Euro-American settlement.

LIMITATIONS

Tree ring data is an integrative index of potential factors dictating growth (water, light, nutrients, etc.). The precise physiological water stress status of these trees is unknown in tree-ring data. Using sap flow and leaf conductance measurements directly or stable isotope data for live and dead trees are essential to determine if stand-level and/or tree-level attributes actually influence tree physiological responses to drought stress. Future research should utilize more direct tree physiology measurements to capture stand- and tree-level influences on drought responses in Sierra Nevada mixed-conifer forests.

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APPENDICES

Appendix A. Trees sampled in each treatment type among all possible live white fir (ABCO) trees at Teakettle Experimental Forest. Sampled trees cover the range of live ABCO trees spectrum by diameter at breast height (dbh, centimeters) and associated competition status in 2017 (Thiessen Polygon Area, meters squared) displaying variation captured in data collection.

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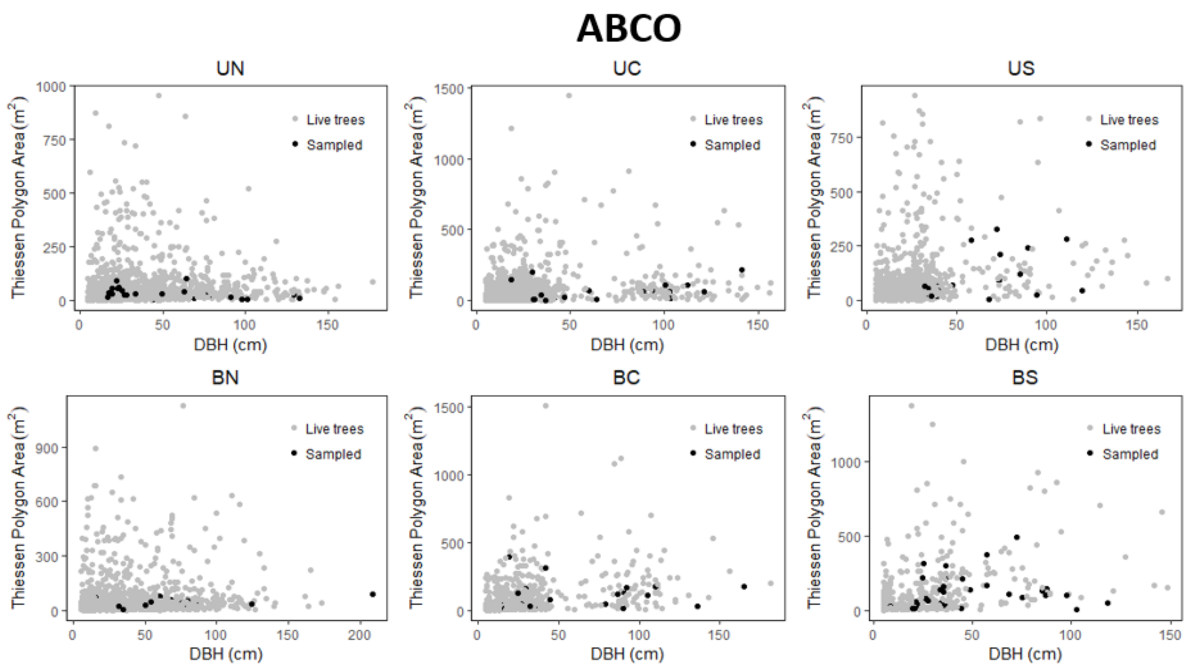
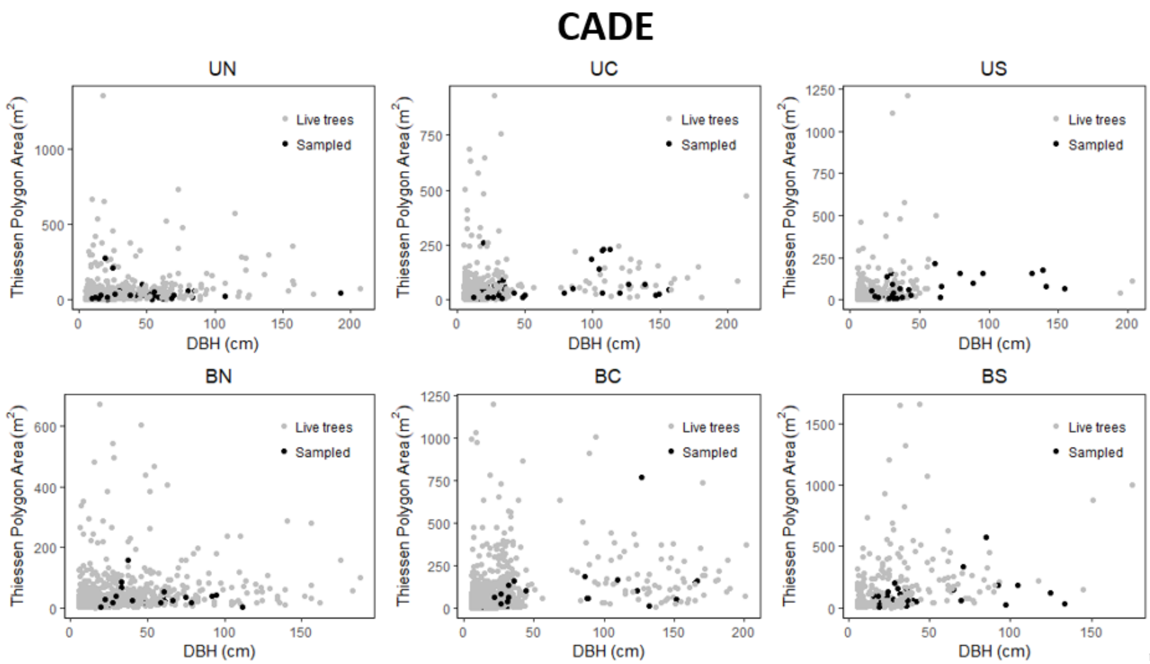
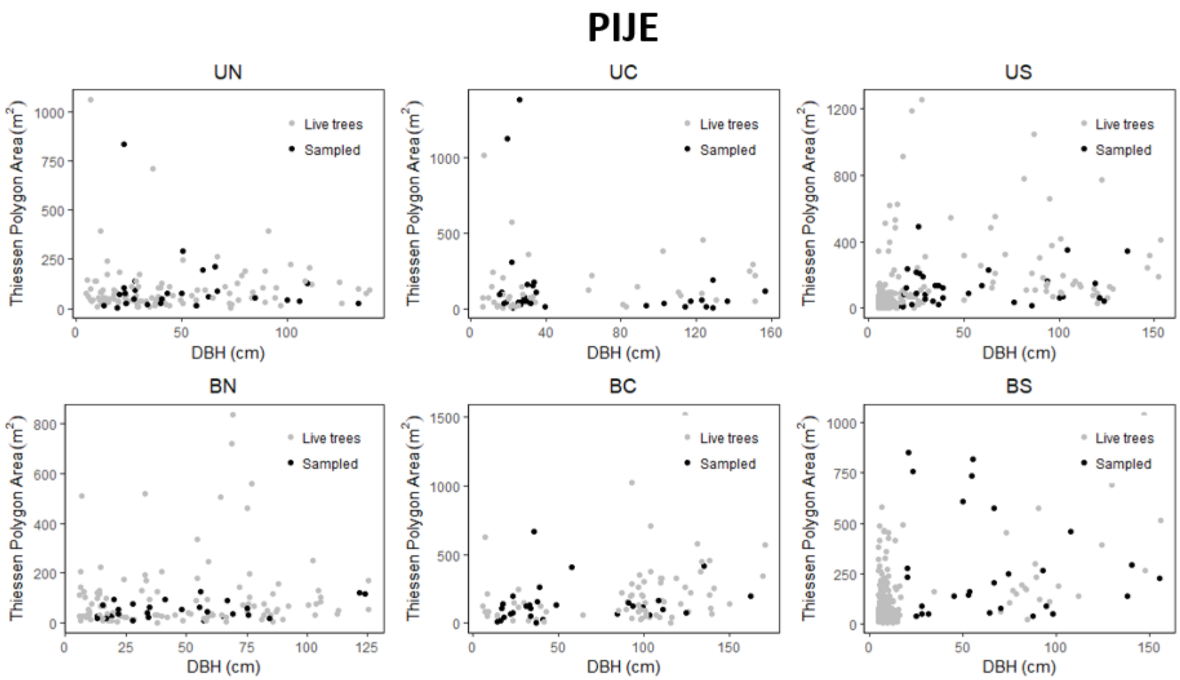


Appendix B. Trees sampled in each treatment type among all possible live incense cedar (CADE) trees at Teakettle Experimental Forest. Sampled trees cover the range of live CADE trees spectrum by diameter at breast height (dbh, centimeters) and associated competition status in 2017 (Thiessen Polygon Area, meters squared) displaying variation captured in data collection.



Appendix C. Trees sampled in each treatment type among all possible live Jeffrey pine (PIJE) trees at Teakettle Experimental Forest. Sampled trees cover the range of live PIJE trees spectrum by diameter at breast height (dbh, centimeters) and associated competition status in 2017 (Thiessen Polygon Area, meters squared) displaying variation captured in data collection.



Appendix D. Trees sampled in each treatment type among all possible live sugar pine (PILA) trees at Teakettle Experimental Forest. Sampled trees cover the range of live PILA trees spectrum by diameter at breast height (dbh, centimeters) and associated competition status in 2017 (Thiessen Polygon Area, meters squared) displaying variation captured in data collection.