

Tree growth responses to extreme drought after mechanical thinning and prescribed fire in a Sierra Nevada mixed-conifer forest, USA

Harold S.J. Zald^{a,*}, Chance C. Callahan^b, Matthew D. Hurteau^c, Marissa J. Goodwin^c, Malcolm P. North^d

^a USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR 97333, USA

^b Cal Poly Humboldt, Department of Forestry and Wildland Resources, Arcata, CA 95521, USA

^c University of New Mexico, Department of Biology, Albuquerque, NM 87131, USA

^d USDA Forest Service, Pacific Southwest Research Station, Mammoth Lakes, CA 93546, USA

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ABSTRACT

An estimated 128 M trees died during the 2012–2016 California drought, largely in the southern Sierra Nevada Range. Prescribed burning and mechanical thinning are widely used to reduce fuels and restore ecosystem properties, but it is unclear if these treatments improve tree growth and vigor during extreme drought. This study examined tree growth responses after thinning, prescribed burning, and extreme drought at the Teakettle Experimental Forest, a historically frequent fire mixed-conifer forest in the southern Sierra Nevada of California, USA. Mechanical thinning (no thin, understory thin, and overstory thin) and prescribed burning (unburned, fall burning) were implemented in 2000–2001. Using annual growth data from increment cores, over 10,000 mapped and measured trees, and lidar-derived metrics of solar radiation and topographic wetness, we had two primary questions. First, what were the growth responses to thinning and prescribed burning treatments, and did these responses persist during the 2012–2016 drought? Second, what tree-level attributes and environmental conditions influenced growth responses to treatments and drought?

Thinning increased residual tree growth and that response persisted through extreme drought 10–15 years after treatments. Growth responses were higher in overstory versus understory thinning, with differences between thinning types more pronounced during drought. Species-specific growth responses were strongest with overstory thinning, with sugar pine (*Pinus lambertiana*) and incense-cedar (*Calocedrus decurrens*) having higher growth responses compared to white fir (*Abies concolor*) and Jeffery pine (*Pinus jeffreyi*). For individual trees, factors associated with higher growth responses were declining pretreatment growth trend, smaller tree size, and post-treatment low neighborhood basal area. Growth responses were initially not influenced by topography, but topographic wetness became important during extreme drought. Mechanical thinning resulted in durable increases in residual tree growth rates during extreme drought over a decade after thinning occurred, indicating treatment longevity in mitigating drought stress. In contrast, tree growth did not improve after prescribed burning, likely due to fire effects that reduced surface fuels, but had little effect on reducing tree density. Thinning treatments promoted durable growth responses, but focusing on stand-level metrics may ignore important tree-level attributes such as localized competition and topography associated with higher water availability. Mechanical thinning was effective at improving growth in trees that had been experiencing declining growth trends, but was less effective in improving growth responses in large old trees of higher ecological importance.

1. Introduction

Globally, accelerated forest mortality has been attributed to

increased drought stress from rising temperatures and water deficits (Allen et al., 2010; Anderegg et al., 2015; Breshears et al., 2009; van Mantgem et al., 2009). The California USA drought of 2012–2016

* Corresponding author at: 3200 SW Jefferson Way, Corvallis, OR 97333, USA.

E-mail addresses: harold.zald@usda.gov (H.S.J. Zald), ccc483@humboldt.edu (C.C. Callahan), mhurteau@unm.edu (M.D. Hurteau), mjgoodwin@unm.edu (M.J. Goodwin), malcolm.p.north@usda.gov (M.P. North).

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(hereafter the California drought) was one of the most extreme droughts in California's recorded history (Robeson, 2015; Williams et al., 2015), among the most severe in the past millennia (Griffin and Anchukaitis, 2014) and was especially notable for its magnitude and impacts on forest ecosystems. From 2010 to 2017, over 129 M trees died in the Sierra Nevada from drought and the compound effects of drought and insect outbreaks (California Department of Forestry and Fire Protection, 2018; Fettig et al., 2019). This multiyear mortality event was unprecedented in magnitude and geographic extent (Stephens et al., 2018), resulting in significant mortality of ecologically important large pine trees (Fettig et al., 2019; Stephenson et al., 2019), adversely impacting federally protected wildlife species (Kordosky et al., 2021), destabilizing forest carbon stores and reallocating forest carbon debt (Earles et al., 2014; Goodwin et al., 2020), and creating fuel conditions conducive to more extreme fire behavior (Goodwin et al., 2021; Stephens et al., 2018). Projected declines in winter snowpack along with increased drought frequency and intensity (Marshall et al., 2019; Ullrich et al., 2018) highlight the need to develop forest management strategies to mitigate the effects of extreme drought on forest mortality and ecosystem services (Millar et al., 2007; Stephens et al., 2020).

Both the direct impacts of drought and the compound impacts of drought and insect outbreaks have been exacerbated by over a century of fire exclusion in the Sierra Nevada. Historically, the yellow pine (*Pinus ponderosa* and *Pinus jeffreyi*) and mixed-conifer forests of the Sierra Nevada were characterized by frequent fire, with a median fire return interval of 7–12 years (Van de Water and Safford, 2011). The elimination of indigenous fire ignitions, logging of large old trees, and aggressive fire exclusion have dramatically increased canopy cover, stand densities, and the spatial continuity of forest fuels (Knapp et al., 2013; North et al., 2007; Parsons and DeBenedetti, 1979; Stephens et al., 2015). These changes in forest structure have increased overall fire severity and the size of high-severity patches (Miller et al., 2009; Stevens et al., 2017), while also making fire-excluded forests more susceptible to drought and endemic bark beetles (Voelker et al., 2019; Young et al., 2017).

Potential management options to mitigate drought impacts are closely linked to those addressing fire exclusion, wildfire risk, and ecosystem restoration. Mechanical thinning and prescribed fire are widely applied in frequent-fire forests to reduce fuels, moderate fire behavior, and restore ecosystem composition, structure, and function (Agee and Skinner, 2005; Fernandes and Botelho, 2003). Mechanical thinning allows for a high degree of treatment specificity with respect to desired forest composition and structure, but financial, logistical, and administrative constraints often limit where thinning can occur (North et al., 2015), resulting in insufficient area thinned in relation to long-term fire deficits (North et al., 2021; Vaillant and Reinhardt, 2017). Prescribed burning can reduce hazardous fuels and restore natural processes with greater economic efficiency (lower cost per unit area) than mechanical thinning, but prescribed fire has its own set of risk, resource, and regulatory constraints (Miller et al., 2020; Quinn-Davidson and Varner, 2012). Reducing tree competition via thinning and/or prescribed burning can mitigate drought impacts by increasing residual tree growth and vigor (Manrique-Alba et al., 2020; Sohn et al., 2016; Tepley et al., 2020; van Mantgem et al., 2020b; Vernon et al., 2018) and reducing tree mortality (Collins et al., 2014; Hood et al., 2016; Knapp et al., 2021; Steel et al., 2021; van Mantgem et al., 2016; Westlind and Kerns, 2021). Longevity of treatment effects on tree vigor is an important consideration, yet most studies are limited to just a few years of post-treatment growth data (van Mantgem et al., 2020b). Additionally, understanding what biotic and abiotic factors mediate treatment effects can help inform the placement and specific implementation of drought mitigation treatments. This may be especially important in frequent-fire, mixed-conifer forests, where multi-scale patterns of topography and vegetation structure play important roles mediating forest productivity (Fricker et al., 2019; Meyer et al., 2007), drought sensitivity (Paz-Kagan et al., 2017), and resilience to wildfire

(Koontz et al., 2020). The importance of these factors suggests treatments for mitigating drought impacts need to be examined at multiple spatial scales.

The objective of this study was to quantify tree growth responses after thinning, prescribed burning, and extreme drought in a mixed-conifer forest in the southern Sierra Nevada of California, USA. A replicated factorial design of mechanical thinning and prescribed burning was implemented in 2000–2001. Using annual growth data from increment cores, over 10,000 mapped and measured trees, and lidar-derived metrics of solar radiation and topographic wetness, we focused on two primary questions. First, what were the growth responses to thinning and prescribed burning treatments, and did these responses persist during the 2012–2016 drought? Second, what tree-level attributes and environmental conditions influenced growth responses to treatments and drought? For the first question we expected growth responses to increase with treatment intensity (i.e. greater reductions in canopy cover, stem densities, and basal area). For the second question we expected local tree competition and topographic wetness to be the greatest drivers of growth responses.

2. Materials and methods

2.1. Study area

The study was conducted within the 1300 ha Teakettle Experimental Forest (TEF), located in the Sierra National Forest, approximately 80 km east of Fresno, California, USA. 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 is Mediterranean, with hot dry summers and cool wet winters, and mean annual precipitation of 125 cm falls almost entirely as snow between November and April (North et al., 2002). Based on Palmer drought severity index (PDSI) values from the California Division 5 of the monthly U.S. Climate Divisional Database (Vose et al., 2014), summer (June–August) PDSI values averaged -0.871 from 1970 to 1994, 2.38 from 1995 to 1999, -0.06 from 2001 to 2006, -1.24 from 2007 to 2011, and -4.95 during the 2012–2016 drought. The mixed-conifer forest at TEF is dominated by white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), sugar pine (*Pinus lambertiana* Dougl.), and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf) with lower densities of red fir (*Abies magnifica* A. Murr.) and California black oak (*Quercus kelloggii* Newberry). Hardwood understory trees such as bitter cherry (*Prunus emarginata* Dougl. ex Hook.), willow (*Salix* spp.), and canyon live oak (*Quercus chrysolepis* Liebm.) are also present.

Prior to experimental treatments, there had been no history of logging or stand replacing disturbance. The last known wildfire at TEF occurred in 1865, before which the mean fire return interval was 17.3 years (North et al., 2005). Prior to fire exclusion, the forest at TEF was characterized by low overall density (67 trees per hectare, tph), equal percentages of shade tolerant and intolerant tree species, a flat diameter distribution, and stems randomly distributed at the stand scale (North et al., 2007). Following fire exclusion, stem density dramatically increased (469 tph) largely comprised of shade-tolerant species (84%), resulting in a reverse J shaped diameter distribution and highly clustered stem distributions (North et al., 2007). Prior to treatments, localized areas of high stem densities were found to influence tree growth-climate relationships and mortality from insects and disease (Hurteau et al., 2007; Smith et al., 2005).

2.2. Treatments and data collection

In 1998, 18 permanent 4 ha treatment units were established in a factorial design, with two levels of prescribed burning (no burn and fall burn) and three levels of thinning (no thin, understory thin, and

overstory thin), for a total of six treatment combinations. Three replicate treatment units were assigned to each treatment combination, with thinning randomly assigned, while burn units were assigned with restricted randomization due to fire line and containment considerations. Thin and burn treatments were thinned in 2000 and burned in 2001, while thin-only treatments were thinned in 2001. Prescribed burning was applied in late October 2001 after the first major rain. Treatment units were individually lit under mild fire weather conditions, resulting in slow creeping ground fire intended to consume surface fuels with little to no overstory mortality (North et al., 2007; Zald et al., 2008). Understory thinning removed trees 25–76 cm in diameter while retaining at least 40% of pre-treatment tree canopy cover. Overstory thinning removed trees greater than 25 cm in diameter, while retaining approximately 22 regularly spaced large diameter trees (generally > 100 cm) per hectare. Prescribed burning alone reduced stand density but not basal area (353.8 tph, 53.7 m² ha) versus unburned no thin controls (469 tph, 56.4 m² ha) (North et al., 2007). Understory thinning alone lowered tree density and basal area (239.5 tph, 41.2 m² ha); with stand density (143.4 tph), but not basal area (37.5 m² ha) further reduced when combined with prescribed burning. Overstory thinning resulted in the lowest stand density and basal area (150.3 tph, 22.7 m² ha), and the combination of overstory thinning and prescribed fire further reduced stand density (93.6 tph), but not basal area (17.2 m² ha). Additional details of treatment effects on forest composition and structure can be found in North et al. (2007).

Prior to treatment implementation (1998–2000 for treated plots, 2001–2002 for control plots) a complete census was conducted of all trees and snags >5 cm diameter at breast height (DBH) within the

treatment units. Trees and snags were permanently tagged, identified to species, diameters measured, and geographic coordinates mapped using a surveyor's total station. All trees were measured in 1999, 2004, 2011, and 2017. In 2017, tree cores and additional tree measurements were collected from a stratified random sample based on the 2011 census data. Sampling strata included all six treatment combinations, the four dominant species (white fir, incense-cedar, sugar pine, and Jeffrey pine), three diameter classes (10–25 cm, 25–55 cm, and >55 cm), and two local competition classes (high versus low competition). Local competition was quantified by generating Thiessen polygons derived from live tree geographic coordinates in the 2011 census, with Thiessen polygon area (m²) around each tree as the metric of competition. Low and high competition classes were based on Thiessen polygon areas greater than or less than the median polygon area within a given treatment combination. Thiessen polygons were used for sampling stratification purposes, but the effects of local competition on growth were quantified using a 10 m radius area around each tree (see Analysis Section below), for consistency with other studies of competition effects on growth and mortality in the Southern Sierra Nevada (Das et al., 2011, 2008; Steel et al., 2021). Five replicate trees were selected randomly for each combination of six treatments, four species, three diameter classes, and two competition classes, resulting in 720 trees sampled across gradients of tree size and localized competition in each treatment combination (Fig. 1). For each sampled tree we recorded the species, diameter, height, live crown ratio, and canopy class (dominant, co-dominant, intermediate, overtopped), and two increment cores were collected at breast height on the uphill and parallel to slope sides of the tree. Two cores were extracted from each tree with a standard 5.15 mm increment

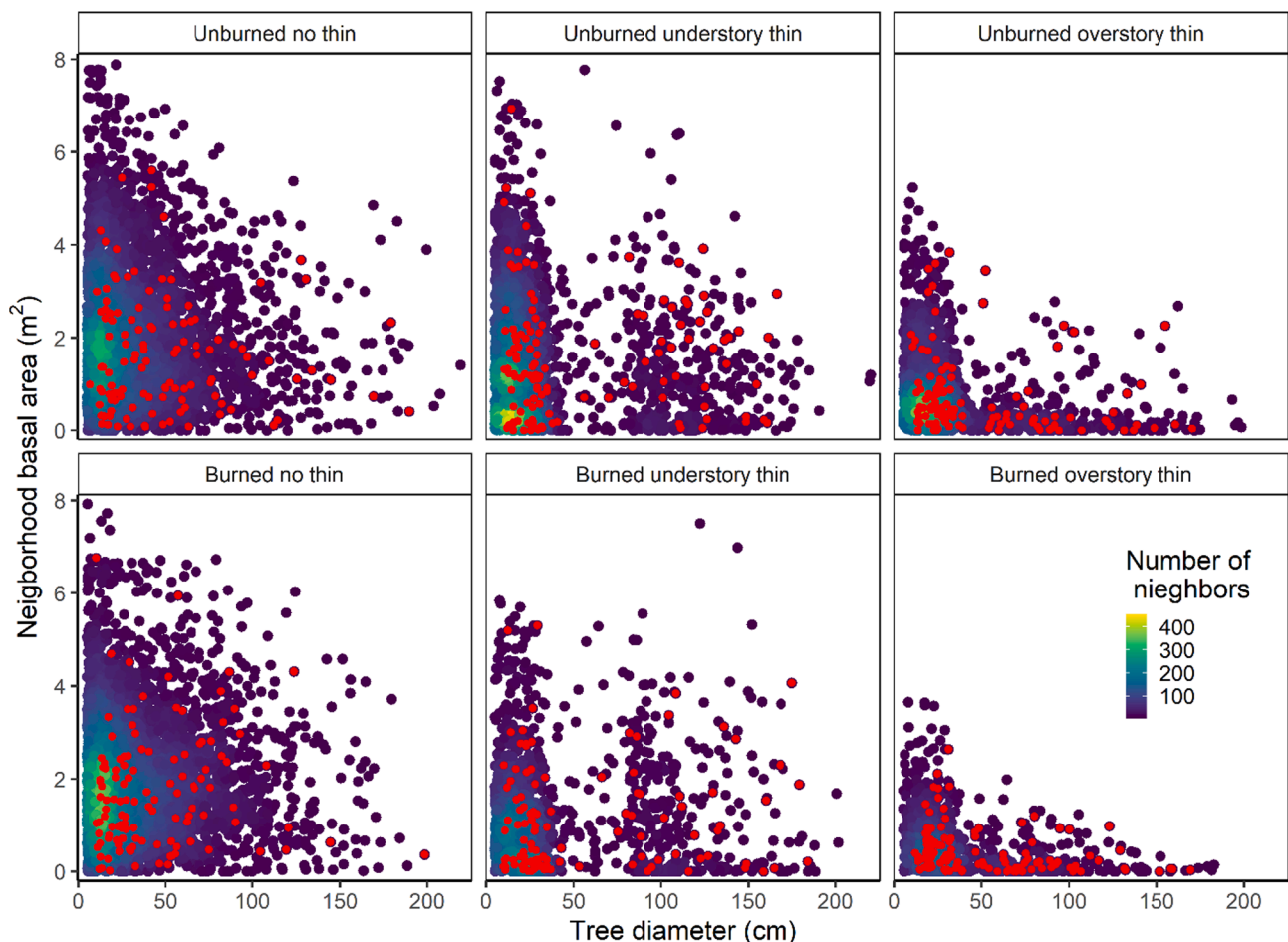


Fig. 1. Sampled trees (red circles) in relation to all live tree diameters and local (10 m) neighborhood basal area within each treatment combination. Unsampled trees colored by density of observations (number of neighbor trees in two dimensional sample space, with lighter regions (yellow) indicating greater number of trees).

borer, except one out of every five replicate trees had its second core collected with a 12 mm diameter increment borer for a companion study of carbon stable isotopes. Cores were taped onto wooden mounting sticks until they dried, then glued and sanded with progressively finer grit sandpaper to visualize tree-ring boundaries. Ring-widths were measured to the nearest 0.001 mm using either a high resolution flatbed scanner with WinDENDRO software (Regent Instruments, Quebec, Canada) or a stereo zoom microscope and Velmex Unislide TA tree-ring measuring system (Velmex, Bloomfield, New York).

Gridded metrics of potential solar radiation and topographic wetness were generated for TEF using a digital terrain model (dtm) derived from airborne discrete return light detection and ranging (lidar) data. Lidar data was collected in October 2010 by Watershed Sciences Inc. (Portland, OR USA) as part of a larger acquisition for the USDA Forest Service. Lidar was collected using dual Leica ALS50 Phase II sensors mounted on a Cessna Caravan 208B flown at 1,100 and 1,500 m above ground level. Lidar survey specifications included a pulse rate of 83 kHz, mirror scan rate of 54 Hz, field of view $\pm 14^\circ$ from nadir, and opposing flight line swath overlap of 50%. Total pulse and ground pulse densities across the entire acquisition area were 8.8 pts/m² and 0.89 pts/m², respectively. We clipped the contractor provided 1 m resolution dtm to the geographic extent of TEF, then used the clipped dtm to calculate potential solar radiation and topographic wetness. Potential solar radiation on a sloping surface was calculated using the Areal Solar Radiation Model in ArcMap 10.7.1 (ESRI, 2019), an insolation model that accounts for atmospheric conditions, elevation, surface orientation, and surrounding topography (Fu and Rich, 2002). Topographic wetness index was calculated using the physically-based basin contribution model (Beven and Kirkby, 1979) using the following Equation:

$$\text{Topographic wetness index} = \ln \frac{\alpha}{\tan \beta + c}$$

where α is the upslope contributing basin area (Moore et al., 1991) calculated with the watershed function in ArcMap, β is the slope at that cell, and c is a small constant ($c = 0.01$) to avoid division by zero in cells with flat terrain. Lower values of topographic wetness indicate greater topographic wetness.

2.3. Analyses

All statistical analyses were conducted in R version 4.1.1 (R Development Core Team, 2020). Tree ring series were cross-dated to ensure correct calendar year assignment of ring-widths using the dplR package (Bunn et al., 2021). Series that could not be cross-dated due to rotten or fragmented cores were discarded, resulting in cross-dated series for 1,401 of the 1,480 cores collected (713 of 740 trees sampled). Annual basal area increment (BAI, mm² yr) was calculated with the dplR package using each tree's ring-width series, tree diameter, and species-specific bark thickness equations (Zeigbig-Kichas et al., 2016) resulting in stem wood annual BAI values excluding bark. We used tree diameters and bark thickness to calculate BAI (versus BAI calculations that only use ring-width increments), to avoid biases in annual BAI calculations that may occur with increment cores that did not reach tree centers, as well as differences in bark thickness between species that likely increase with tree size. Series annual BAI values were then averaged for paired cores to calculate annual mean BAI for each tree.

Three different growth response metrics were calculated from annual BAI values to quantify the short-term (Rtrt_s) and mid-term (Rtrt_m) responses to treatments, as well as the growth response to treatments during the drought (Rtrt_d). Rtrt_s was calculated as the 2002–2006 mean annual BAI divided by the 1995–1999 pretreatment mean annual BAI. Rtrt_m was calculated as the 2007–2011 mean annual BAI divided by the pretreatment mean annual BAI. Rtrt_d was calculated as the 2012–2016 mean annual BAI divided by the pretreatment mean annual BAI. The choice of 1995–1999 pretreatment years avoided wetter than average

growth years, and 2002–2006 were selected for short-term growth response to avoid immediate post-treatment abnormalities in growth that can occur due to shock, mechanical damage, and fire damage (Agee and Skinner, 2005; Harrington and Reukema, 1983). Resistance and resilience metrics are commonly used to quantify growth responses to drought and disturbance events (Lloret et al., 2011). However, the value of these metrics can vary depending on time intervals selected (Schwarz et al., 2020), which can be problematic in the context of multi-year drought events. Furthermore, resistance metrics calculated using growth conditions immediately preceding a drought may lack the context of how previous disturbances and management activities altered growth leading up to and during drought. We believe this is a critical distinction as our study focused on the effects of treatments on growth, and the persistence of those treatment effects during the drought, so we did not calculate resistance or resilience metrics.

We evaluated the effects of thinning, burning, and species on growth response metrics with linear mixed effects (LME) models using the nlme package (Pinheiro et al., 2020). Response variables (Rtrt_s, Rtrt_m, Rtrt_d) were log transformed after histograms, quantile–quantile plots, and Shapiro-Wilk's tests found violations of linearity and normality. LME models included three fixed effects (burn, thin, species) and all possible interactions among them. Individual treatment units were included as a random effects term. Estimated marginal means and pairwise comparisons for all significant fixed effects and significant interactions were calculated using the emmeans package (Lenth et al., 2018). Estimated marginal means of response values were back transformed, 95% confidence intervals calculated for marginal means and contrasts between fixed effects levels, and 95% confidence intervals and p-values using Tukey's adjustment for multiple comparisons used to evaluate significance of contrasts.

We assessed the relative importance and relationships between tree-level growth response metrics and potential predictor variables using the Random Forest (RF) supervised machine learning algorithm with the randomForest package (Liaw and Wiener, 2002). Separate RF models were created for each of the three growth response metrics. Predictor variables included thin, burn, tree characteristics, tree competition, solar radiation, and topographic wetness. Tree characteristics included species, diameter, height, live crown ratio, pretreatment growth trend, and pretreatment number of abrupt growth declines. We used tree diameters instead of tree ages from increment cores for multiple reasons. Relationships between tree diameters and ages can be highly variable (Loewenstein et al., 2000; Nagel et al., 2007; Veblen et al., 1991), but we found moderate to high correlations between diameters and ages for all four species in our study (Fig. 2). The 5.15 mm diameter increment borers we used had a maximum length of 71 cm, resulting in borers only capable of reaching the center of trees less than 142 cm in diameter, less than the largest trees at TEF. Since the focus of this study was not reconstruction of stand ages, we did not apply commonly used pith correction methods (Applequist, 1958; Duncan, 1989). Uncertainty in tree ages can have important consequences for accuracy of and inference from stand reconstructions (Fahey and Lorimer, 2014). However, in our study we are more interested in large trees being generally older than small trees, and the importance of large old trees for carbon sequestration and wildlife habitat (North et al., 2017; Stephenson et al., 2014). Pretreatment growth trends and abrupt growth declines were both calculated from tree annual BAI series and were included as potential predictor variables because growth declines are often associated with conifer tree vigor and mortality (Cailleret et al., 2017; van Mantgem et al., 2020a). Annual BAI for the 1970–2000 time period for each tree was standardized by its respective mean and standard deviation to account for different growth rates associated with tree size. A linear model was then fit to each tree's standardized annual BAI during the 1970 to 2000 time period, with the slope coefficient of the linear model representing pretreatment growth trend. The number of pretreatment abrupt growth declines within a tree was calculated as the number of year-to-year declines in annual BAI exceeding 50% during the 1970–2000

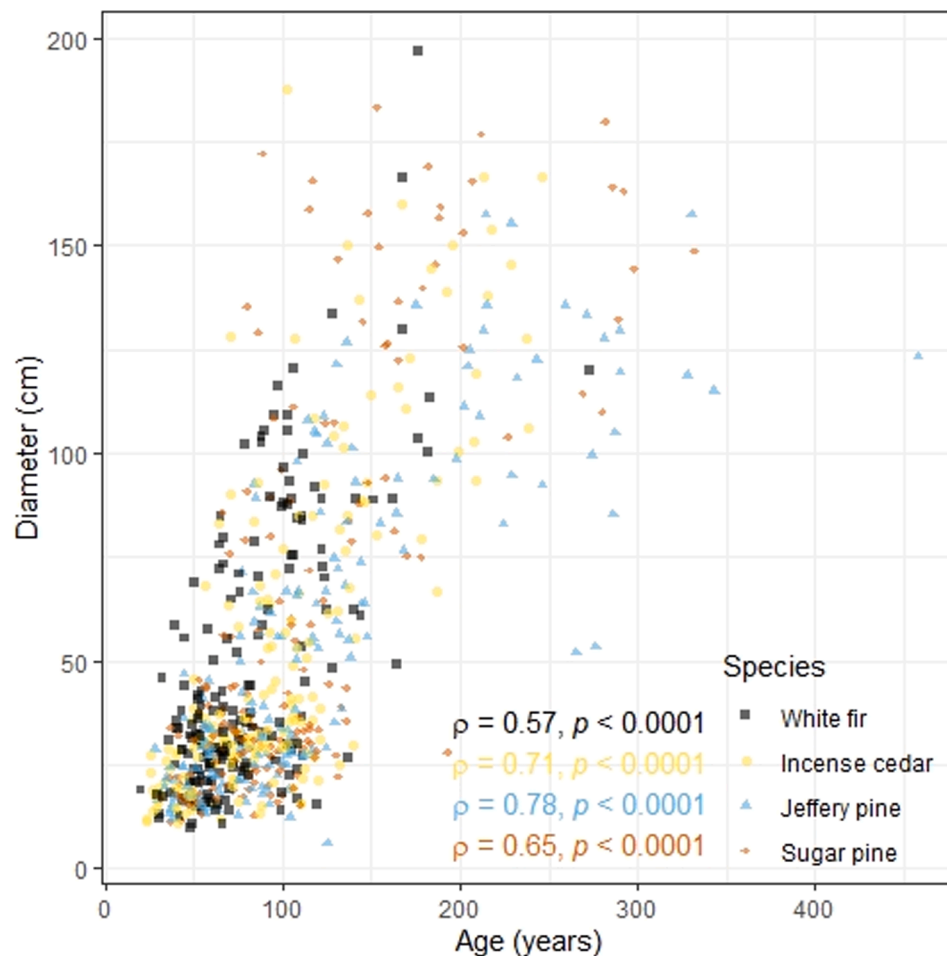


Fig. 2. Relationship between diameter and ring count (age) by species for sampled trees. Spearman correlation coefficients (ρ) and associated p values (p) of the relationship between tree diameters and ages are color coded by species.

time period. Tree competition was calculated from the 2011 census data. Following other studies in Sierra Nevada mixed-conifer forests, we defined local competition as a 10 m radius around the target tree (Das et al., 2011, 2008; Steel et al., 2021). For the 10 m radius around each tree, the basal area of all trees, trees less than 25 cm diameter, and trees greater than 25 cm diameter was calculated. Mean annual solar radiation and topographic wetness index were also calculated within a 10 m radius around each tree.

RF models were applied with 1,500 bootstrap samples. For each of the three RF models, we calculated variable importance values for each predictor variable as the percent increase in the mean squared error (MSE) in the predicted response variable when values for the predictor were permuted and all other predictors unaltered. In addition to variable importance values, we determined which predictor variables should be retained in each RF model using a two-stage variable selection for interpretation using the VSURF package (Genuer et al., 2019). Final RF models were then run including only the selected predictor variables. The relationships of selected predictor variables on tree growth response metrics in the final RF models were visualized using partial dependency plots (Friedman et al., 2001).

3. Results

3.1. Stand-level growth responses

Standardized basal area increments (sBAI) were highly variable between trees over time, but displayed clear increases following thinning (Fig. 3). Short-term and mid-term growth responses ($Rtrt_s$ and $Rtrt_m$)

varied by thinning, species, and the interaction of thinning and species, but not burning or the interaction of burning and thinning (Table 1, Fig. 4). Thinning and the interaction of thinning and species were also significant for growth responses during drought ($Rtrt_d$). Relative to no thin units, understory thinning increased growth responses for $Rtrt_s$ ($t = 9.01$, $p < 0.0001$), $Rtrt_m$ ($t = 10.05$, $p < 0.0001$), and $Rtrt_d$ ($t = 12.91$, $p < 0.0001$). Compared to pretreatment (1995–1999), the estimated marginal mean basal area increment after understory thinning was 1.56 times greater in 2002–2006 (1.44–1.70 95% CI), 2.20 times greater in 2007–2011 (1.99–2.43 95% CI), and 2.02 times greater in 2012–2016 (1.81–2.25 95% CI). Overstory thinning increased growth responses versus understory thinned units, and this persisted for all time periods ($Rtrt_s$ $t = 4.68$, $p = 0.0014$; $Rtrt_m$ $t = 4.43$, $p = 0.0022$; $Rtrt_d$ $t = 4.01$, $p = 0.0045$). Compared to pretreatment (1995–1999), the estimated marginal mean basal area increment after overstory thinning was 2.01 times greater in 2002–2006 (1.85–2.18 95% CI), 2.94 times greater in 2007–2011 (2.66–3.26 95% CI), and 2.70 times greater in 2012–2016 (2.41–3.02 95% CI). Prescribed burning only had suggestive effects of lower growth responses versus unburned units for $Rtrt_s$ (ratio = 1.08, 0.99–1.19 ratio 95% CI, $t = 1.84$, $p = 0.0901$) and $Rtrt_m$ (ratio = 1.11, 0.98–1.25 ratio 95% CI, $t = 1.89$, $p = 0.0828$), and $Rtrt_d$ (ratio = 1.11, 0.97–1.26 ratio 95% CI, $t = 1.75$, $p = 0.1064$).

Species differences in growth responses were found after treatment ($Rtrt_s$ and $Rtrt_m$) but not during the drought ($Rtrt_d$), with higher growth responses for incense-cedar versus Jeffrey pine in 2002–2006 ($t = 2.76$, $p = 0.0299$), and higher growth responses for incense-cedar versus white fir ($t = 2.85$, $p = 0.0231$) in 2007–2011. However, species differences appear to be driven by the interaction with thinning (Table 1,

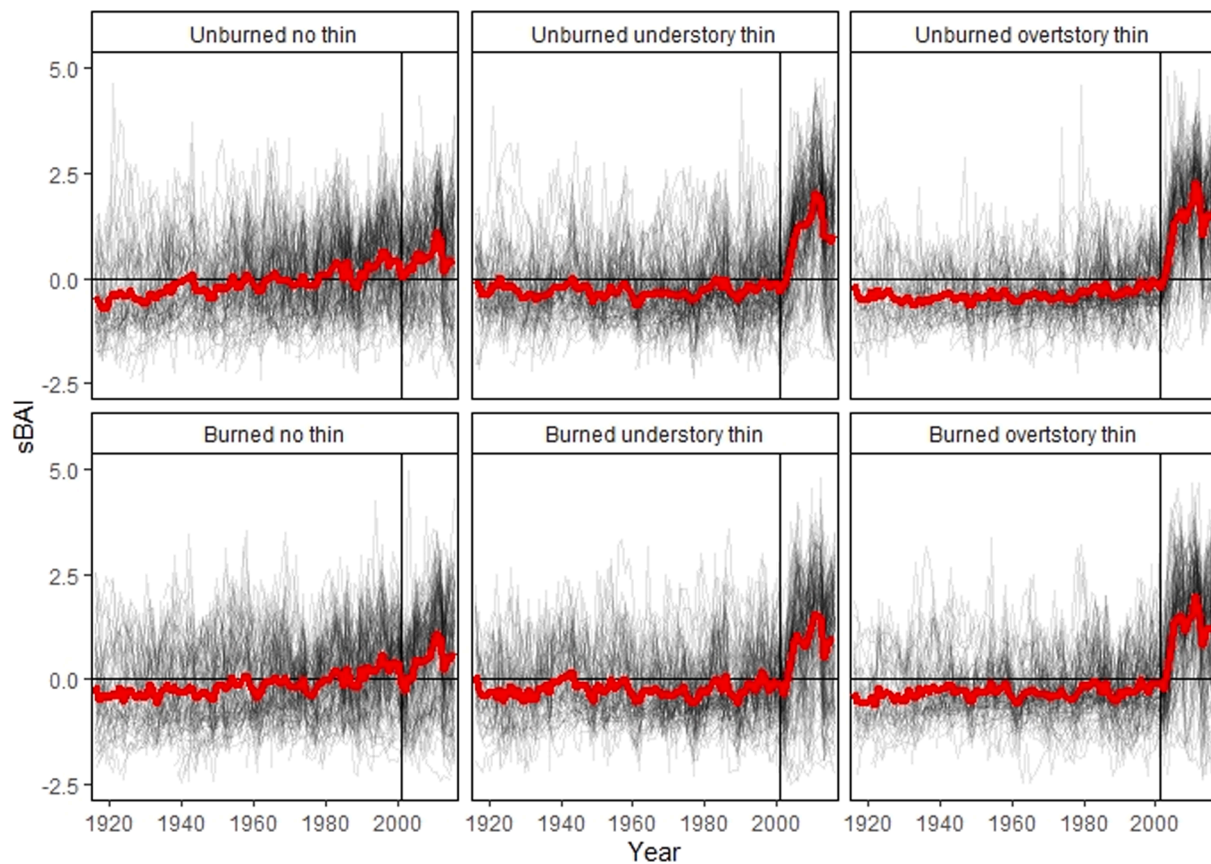


Fig. 3. Growth trends by treatment combination over time. Individual tree (gray lines) and average (red line) are standardized annual basal area increments (sBAI) over time. Vertical black line denotes year of treatment (2001).

Table 1

Fixed effects on growth responses in linear effects models. Note: Growth metrics are short-term after treatment ($Rtrt_s$), mid-term after treatment ($Rtrt_m$) and during drought ($Rtrt_d$).

Growth metric	Fixed effect	numDF	denDF	F value	p value
$Rtrt_s$	burn	1	12	3.80	0.0750
	thin	2	12	94.64	0.0000
	species	3	676	2.91	0.0340
	burn:thin	2	12	0.36	0.7051
	burn:species	3	676	1.98	0.1163
	thin:species	6	676	2.81	0.0105
	burn:thin:species	6	676	0.83	0.5446
$Rtrt_m$	burn	1	12	4.31	0.0601
	thin	2	12	108.06	0.0000
	species	3	676	3.57	0.0139
	burn:thin	2	12	2.36	0.1362
	burn:species	3	676	1.55	0.2003
	thin:species	6	676	3.18	0.0043
	burn:thin:species	6	676	1.03	0.4066
$Rtrt_d$	burn	1	12	3.68	0.0790
	thin	2	12	87.29	0.0000
	species	3	676	2.36	0.0702
	burn:thin	2	12	2.38	0.1343
	burn:species	3	676	1.18	0.3160
	thin:species	6	676	2.30	0.0335
	burn:thin:species	6	676	0.71	0.6379

Fig. 4. Within overstory thinning, Jeffery pine had a lower short-term growth response ($Rtrt_s$) than incense-cedar ($t = 4.60$, $p < 0.0001$) and sugar pine ($t = 3.05$, $p = 0.0129$), and suggestively lower than white fir ($t = 2.56$, $p = 0.0522$). Mid-term growth responses ($Rtrt_m$) continued to be lower for Jeffery pine versus incense-cedar ($t = 4.50$, $p < 0.0001$) and sugar pine ($t = 3.22$, $p = 0.0074$), while white fir also had lower mid-

term growth response versus incense-cedar ($t = 3.43$, $p = 0.0036$). During the drought, growth responses ($Rtrt_d$) of Jeffery pine continued to be lower than incense-cedar ($t = 3.59$, $p = 0.0020$) and sugar pine ($t = 2.88$, $p = 0.0214$), while white fir continued to have a lower growth response versus incense-cedar ($t = 2.74$, $p = 0.0320$).

3.2. Tree-level growth responses

Two-stage variable selection procedures retained 6–8 variables in the final RF models describing tree-level growth responses (Fig. 5). For final RF growth response models, pretreatment growth trend was the most important predictor variable, increasing mean squared error (MSE) in the final RF models by 55.50% for $Rtrt_s$, 47.64% for $Rtrt_m$, and 25.67 for $Rtrt_d$. Following pretreatment growth trends in declining importance were tree diameter, thinning treatment, tree height, neighborhood basal area of trees greater than 25 cm in diameter, neighborhood basal area of all trees, topographic wetness index, and neighborhood basal area of trees less than 25 cm in diameter. Neighborhood basal area of trees greater than 25 cm in diameter and topographic wetness index were only important for $Rtrt_d$. Variance described by final RF models declined over time, with 34.7%, 33.5%, and 21.84% of variance described for $Rtrt_s$, $Rtrt_m$, and $Rtrt_d$, respectively.

Partial dependency plots of final RF models displayed clear relationships between growth responses and predictor variables (Fig. 6). Trees with negative pretreatment growth trends had higher growth responses than trees with positive pretreatment growth trends, although trees with slightly negative to slightly positive pretreatment growth trends had the largest positive growth responses, and positive growth responses were greater for $Rtrt_m$ and $Rtrt_d$ versus $Rtrt_s$. Medium and smaller trees (less than 50 cm in diameter, less than 20 m tall) had greater growth responses and these growth responses were greater for

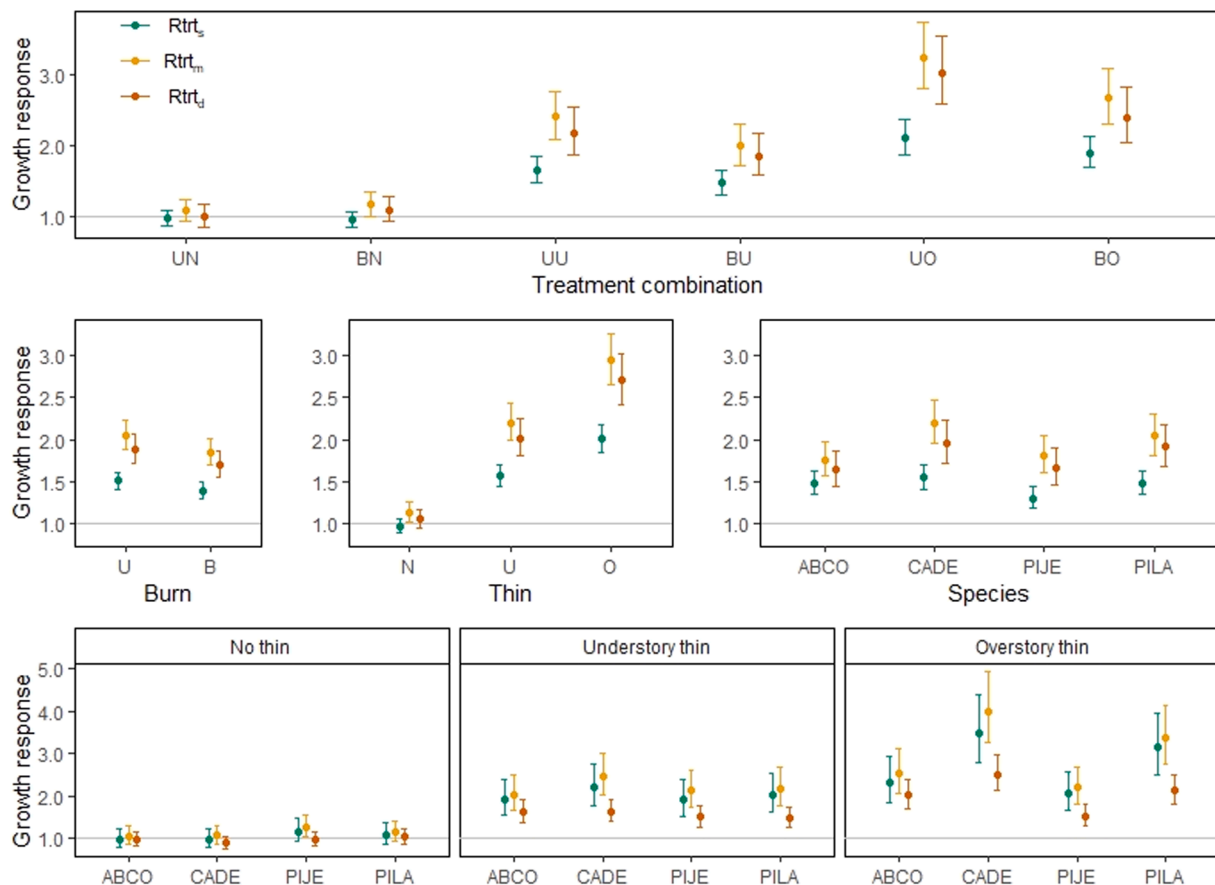


Fig. 4. Estimated marginal means and 95% confidence levels (error bars) of growth responses to burning, thinning, species, burning $\times$ thinning interaction, and species $\times$ thinning interaction. Growth responses greater than 1 denote greater basal area growth versus pretreatment. Growth responses are for short-term after treatment ($Rtrt_s$, green), mid-term after treatment ($Rtrt_m$, orange), and after treatment during drought ($Rtrt_d$, red). Burn treatments were unburned (U) and burned (B). Thinning treatments were no thin (N), understory thin (U), and overstory thin (O). Species were *Abies concolor* (ABCO), *Calocedrus decurrens* (CADE), *Pinus jeffreyi* (PIJA), and *Pinus lambertiana* (PILA).

$Rtrt_m$ and $Rtrt_d$ versus $Rtrt_s$. Growth responses were lower for medium to large large trees, but they still had greater growth following treatment (growth response > 1). As in the stand-level LME models, tree-level growth responses were greatest with overstory thinning, followed by understory thinning, and no thinning. High growth responses were associated with low neighborhood total basal area ($< 0.5 \text{ m}^2$ within 10 m), but once basal area was greater than 1 m^2 there was little effect on growth responses. Neighborhood basal area of large trees (greater than 25 cm diameter) and small trees (less than 25 cm diameter) had a similar but much reduced effect on growth responses. There was a gradual increase in growth responses with high neighborhood basal area, but these trends in partial dependency plots are poorly supported by the small sample size of trees with the highest neighborhood basal area values. Topographic wetness was only important for growth responses during the drought, during which wetter conditions (lower topographic wetness index values) were associated with higher growth responses.

4. Discussion

Tree growth is an important proxy for tree vigor and predicting future mortality (Cailleret et al., 2017). The response of tree growth to forest practices is an important indicator of the potential for management to mitigate the increasing drought stress that is occurring with changing climate (Ullrich et al., 2018; Williams et al., 2019). Positive growth responses to thinning and burning treatments designed to moderate fire behavior would indicate that in frequent-fire forests, treatments to reduce the risk of high-severity fire could also increase tree

growth resistance and resilience to drought. We found mechanical thinning increased residual tree growth six to ten years after treatment, and increased growth was sustained during extreme drought fifteen years after treatments. Initial growth responses during the first five years after treatments were lower than six to ten years posttreatment or during the drought 11 to 15 years after treatment. Delayed stem wood growth responses to thinning have been documented in other forest types (Latham and Tappeiner, 2002; Skov et al., 2005), with temporal differences between stem wood production and physiological processes such as stomata conductance and net photosynthesis suggesting initial allocation of resources towards root formation versus stem wood (McDowell et al., 2003; Skov et al., 2004), and highlighting the importance of longer-term growth data to assess treatment efficacy. Greater thinning intensity (overstory versus understory thinning) was associated with greater stand-level growth response, while prescribed burning had little effect on growth responses. Pretreatment growth trends were the most important variable influencing tree-level growth responses to treatment and drought, followed by tree diameter, mechanical thinning, tree height, and local competitive environment. It is important to note live trees were sampled in 2017, therefore growth responses presented are conditional upon surviving the 2012–2016 drought. However, using the same tree census data, thinning was found to reduce drought and insect driven forest mortality (Steel et al., 2021), indicating mechanical thinning can mitigate both growth and mortality effects of extreme drought in these forests. Our results are consistent with individual trees responding to changes in moisture availability and species-specific plastic responses to drought. These two mechanisms are

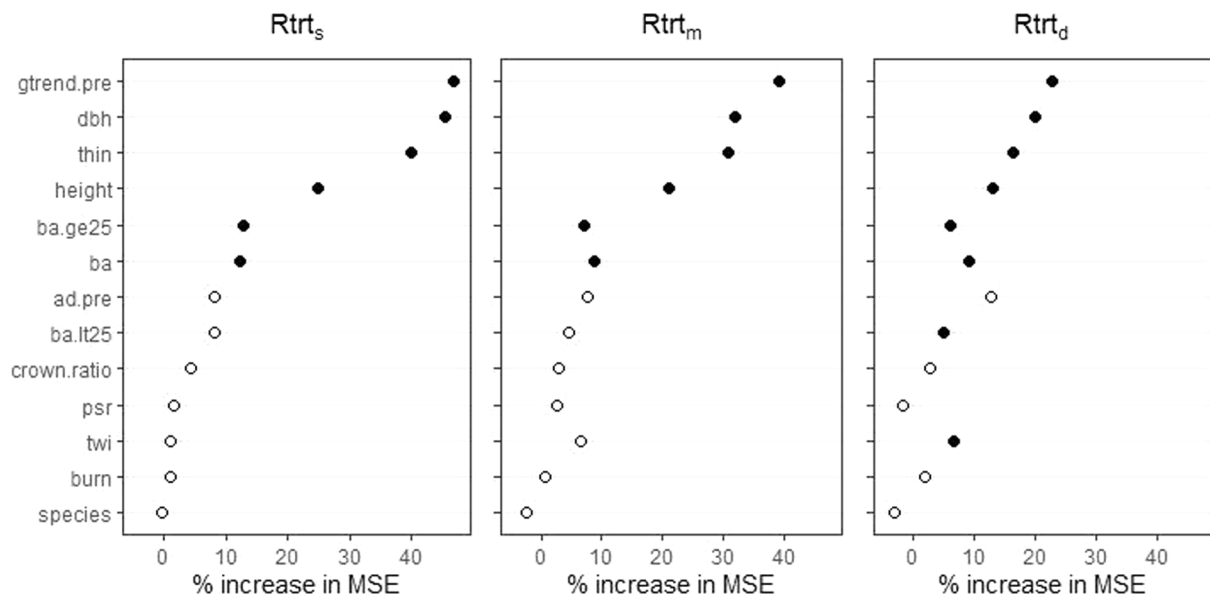


Fig. 5. Variable importance plots for predictor variables from Random Forest (RF) models of growth response metrics. Short-term growth response to treatment ($Rtrt_s$, left panel), mid-term growth responses to treatment ($Rtrt_m$, center panel), and growth response to treatment during drought ($Rtrt_d$, right panel). Variable importance as measure by percent increase in mean squared error (MSE). Solid circles denote variables retained in two-stage variable selection procedures, open circles denote variables removed from the final RF models during variable selection. Predictor variables include pretreatment growth trend (gtrend.pre), diameter (dbh), level of thinning (thin), tree height neighborhood basal area of trees greater than 25 cm dbh (ba.ge25), neighborhood basal area of all trees (ba), neighborhood basal area of trees less than 25 cm dbh (ba.lt25), number of abrupt growth declines prior to treatment (ad.pre), live crown ratio (crown.ratio), potential solar radiation (psr), topographic wetness index (twi), levels of burning (burn), and tree species (species).

likely operating simultaneously and the attribution of one mechanism over another to tree growth may differ from the stand-level to the tree-level.

4.1. Stand-level growth responses to thinning and prescribed burning

Studies have found enhanced growth and physiological resistance to extreme drought shortly after thinning and/or prescribed burning treatments (Keen et al., 2022; Tepley et al., 2020; van Mantgem et al., 2016; Vernon et al., 2018). Our study found growth responses over a decade after mechanical thinning treatments. Treatment longevity is an important consideration for broader applicability of thinning in frequent-fire forests, in which fuel reduction and drought mitigation objectives are often linked. Treatments designed to reduce the surface fuel loads and their spatial continuity to moderate fire behavior must be effective and durable over time, since it is not possible to predict the timing and location of specific fires. Likewise, long lasting effects of treatments for drought mitigation are a prerequisite to increasing the proportion of the landscape effected. Our findings suggest mechanical treatments can be effective at mitigating extreme drought effects on tree growth for at least a decade in this mixed-conifer forest, and likely longer given the magnitude of growth responses observed 11–15 years after treatment. These growth responses are comparable to the longevity of thinning effects on fuels and fire behavior in Sierra mixed-conifer forests (Low et al., 2021; Stephens et al., 2012), indicating the objectives of fuel reduction and drought mitigation are temporally compatible.

Growth responses were greater in overstory versus understory thinning, consistent with lower competition via greater reductions in stand density and basal area (North et al., 2007). Additionally, species-specific growth responses only manifested with overstory thinning, where incense-cedar and sugar pine had greater growth responses compared to white fir and Jeffrey pine. However, caution should be applied to species-specific responses, as they may reflect intrinsic species differences in utilizing available resources after treatment, or topographic and forest structural conditions unrelated to treatments. For example, sugar

pinos have relatively high plasticity to environmental conditions, with decreasing shade tolerance as they age (Harlow et al., 1996), resulting in strong growth declines with increased shading of non-dominant trees, and strong growth responses to heavy thinning and gap creation (McDonald, 1976). In contrast, Jeffrey pine occupies more open xeric sites where available moisture may come from bedrock fissures (Hubbert et al., 2001; Hurteau et al., 2007), suggesting forest competition or its reduction via thinning are less responsible for its growth responses to treatments. Stronger growth responses of incense-cedar versus white fir were somewhat unexpected, as white fir growth has been found to be more sensitive to interannual climate variation and its mediation via competition (Hurteau et al., 2007). However, differences in the hydraulic and stomatal regulation strategies of these two species could contribute to these differences in growth responses (Bigelow et al., 2014; Hochberg et al., 2018). For example, an investigation of conifer traits and functional strategies found incense-cedar had higher growth rates than pines on drier sites, suggesting that incense-cedar may be more drought-tolerant than other conifer species (Buotte et al., 2021). Further, species-specific differences in primary water source and water use strategies could also result in differences in growth due to increased dependence on water stored in highly porous weather and fractured bedrock during drought (Klos et al., 2018).

Our data show that prescribed burning had suggestive lower growth responses and no interactive effects with thinning, consistent with other recent studies showing persistent growth increases after thinning, but little added effect of prescribed burning (Knapp et al., 2021; Tepley et al., 2020). It is important to consider the role of fire in this ecosystem, the effects of decades of fire exclusion preceding our experimental burn, and the manner in which our experimental burn was applied. In pine species, the combination of thinning and prescribed fire can increase growth and resin defenses (Hood et al., 2015, 2016), but prescribed burning can also result in short-term reductions in tree growth from damage to cambium, live crowns, and roots (Busse et al., 2000; Collins et al., 2014; Lloret et al., 2011). The last widespread surface fire at TEF was in 1865 (North et al., 2005) and high surface fuel accumulation and increased density over the following 150 years increased the likelihood

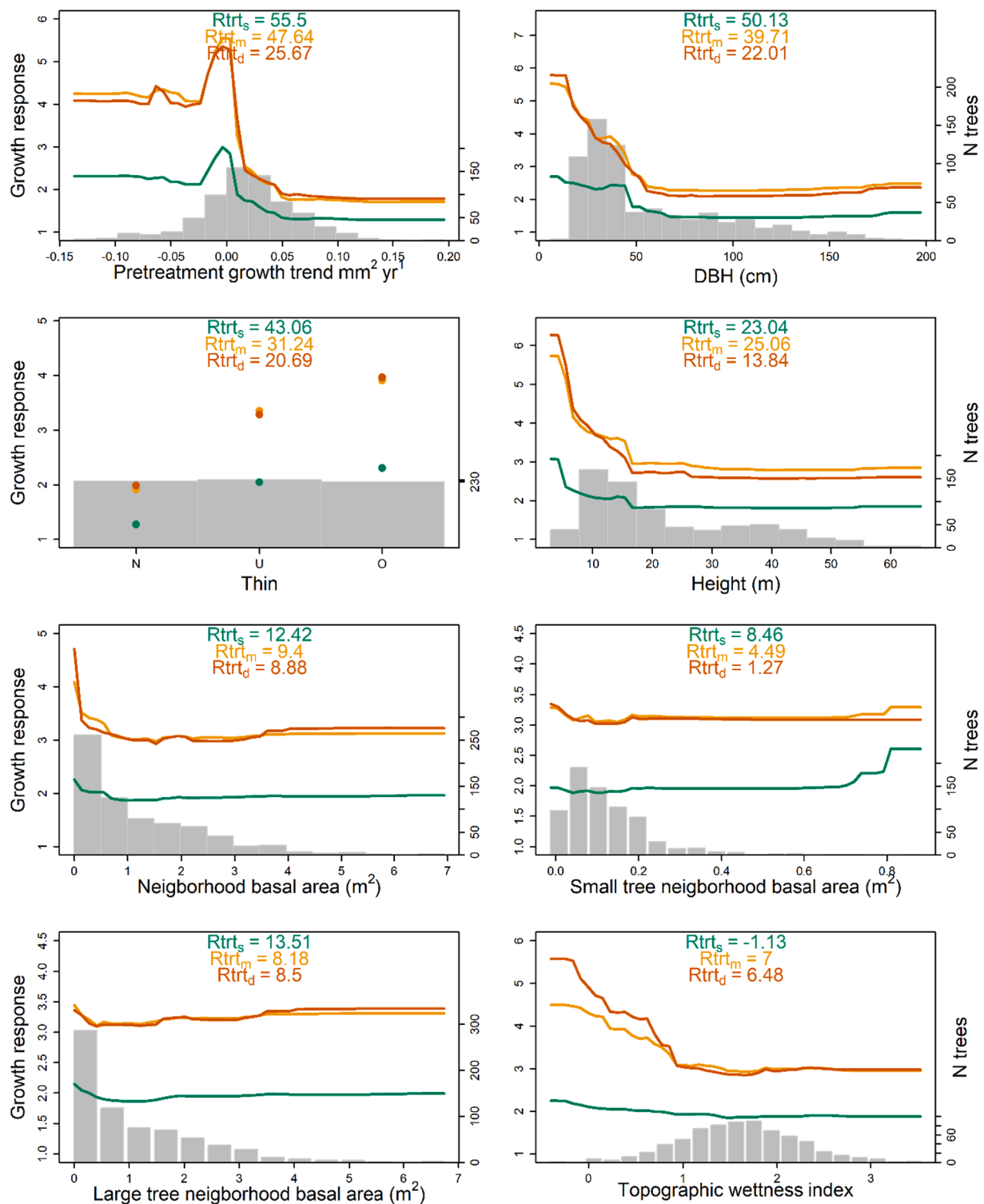


Fig. 6. Partial dependency plots showing relationships between each predictor variable and growth responses metrics in random forest models. Short-term growth response to treatment ($Rtrt_s$, green), mid-term growth responses to treatment ($Rtrt_m$, orange), and growth response to treatment during drought ($Rtrt_d$, red). Numbers within each panel show variable importance values by growth responses metric. Solid lines show trends in growth response metrics in relation to predictor variables. Histograms (gray bars) show the distribution of values for each predictor variable.

of experiencing injury from sustained basal heating and/or burning of fine root growth within the organic soil layer. In addition to the potentially negative direct effects of prescribed burning, it is unlikely the fire reduced competition in our study. Prescribed burning at TEF occurred under mild fire weather conditions to meet objectives of consuming surface fuels and small trees while avoiding overstory

ignition (Zald et al., 2008) and had little effect on basal area, canopy cover, and diameter distributions (North et al., 2007). In contrast, a nearby study in the southern Sierra Nevada on USDI National Park Service lands found prescribed burning can reduced stand densities and drought associated tree mortality (van Mantgem et al., 2021). This highlights the need for prescribed burning to move beyond strict fuel

reduction (Collins et al., 2014) and include density reduction objectives that can increase tree vigor (North et al., 2022, 2021).

4.2. Tree-level growth responses

Pretreatment growth trends were the most important predictor of growth responses, with trees with declining growth prior to treatment having greater growth responses after treatment. This finding was somewhat unexpected as others have found pre- and post-treatment growth to be positively correlated (Hood et al., 2018), but nonetheless our results are encouraging as declining growth often precedes tree mortality (Cailleret et al., 2017). It appears competition release with mechanical thinning most benefited trees with declining vigor and greater competitive stress. Individual tree growth responses were strongly affected by tree size, with smaller trees (less than 50 cm DBH and 20 m tall) having greater growth responses both after treatment and during the drought. Older tall trees often have reduced photosynthetic rates that are likely driven by hydraulic limitation and associated compensatory mechanisms (Hubbard et al., 1999; McDowell et al., 2002; Ryan and Yoder, 1997; Yoder et al., 1994), suggesting larger and older trees may be intrinsically less able to use resources made available by thinning. However, caution should be applied to interpreting these findings as large older trees responded poorly to thinning. Partial dependency plots consistently showed growth response values greater than one, with large trees in excess of 100 cm DBH and 30 m tall having positive growth responses to treatments, even during drought. Radial growth patterns are broadly used as proxies for tree vigor, but they should be placed in the context of objectives which may vary based on tree size and age. Maximizing growth and carbon sequestration rates may be valid objectives for younger and smaller trees. However, regional and global declines of large old trees that provide critical ecosystem functions (Lindenmayer et al., 2014; Lutz et al., 2009; van Mantgem and Stephenson, 2007) suggest a more conservative objective of maintaining vigor and reducing mortality is warranted for old large trees, but it is unclear if more modest growth responses to thinning achieve this.

Compared to the strong effects of pretreatment growth trends, thinning treatments, tree size, local basal area competition, and topographic wetness had minor effects on tree-level growth responses. Growth responses to local competition appeared to only increase when local (10 m radius) basal area was less than 1 m², with the greatest increases in growth responses when local basal area was below 0.5 m². These levels of localized basal area correspond to 31.8 and 15.9 m² ha⁻¹, and are consistent with recent studies suggesting low levels of localized competition are likely needed to promote tree vigor and resilience to drought, fire, and insect outbreaks (Furniss et al., 2021; Hood et al., 2018; North et al., 2022). However, it is important to recognize such density reductions should occur while maintaining and restoring the structural heterogeneity that characterized Sierra Nevada mixed-conifer forests prior to fire exclusion (Fry et al., 2014; Lydersen et al., 2013; North et al., 2007). Forest productivity and vegetation heterogeneity in these forests is in part mediated by soil and topography at multiple spatial scales (Beatty and Taylor, 2008; Jeronimo et al., 2019; Meyer et al., 2007; Ng et al., 2020). While topographic wetness was not a significant driver of growth responses in the first decade after treatments, it did become a significant (albeit minor) driver of growth responses during the drought. This may reflect the magnitude of drought needed for topographically mediated moisture availability to become important.

4.3. Management implications and limitations

Strong stand-level growth responses to overstory thinning, and tree-level growth responses to low levels of neighborhood basal area, suggest treatments that greatly reduce basal area may be needed to promote growth resistance to extreme drought. Additionally, our findings suggest

reducing competition may be most beneficial on topographically wetter sites. However, these findings should be placed in the context of existing knowledge about vegetation structure in these forests, as well as potential conflicts between different management objectives. Spatial heterogeneity of vegetation is a defining feature of these forests under an active fire regime (Fry et al., 2014), with restoration of structural heterogeneity a broad management objective (North et al., 2009). This would suggest high levels of basal area reduction should also reduce the size of large high-density patches and increase the area of gaps and single trees between high-density patches. At the same time, our finding that wetter topographic sites may benefit more from basal area reduction suggests the largest benefits of thinning for tree growth and drought resistance could be in conflict with management of sensitive wildlife species (North et al., 2009; Underwood et al., 2010). Growth responses to local density reduction that may be a function of landscape position that reflects water availability in highly porous weathered and fractured bedrock. Additional investigation into the contribution of this water source to sustained growth and reduced mortality during drought is an important area for additional investigation (Goulden and Bales, 2019; Preisler et al., 2019). Lastly, our results suggest larger trees are less responsive to competition reduction, but our growth metric based on changes in annual basal area increment may be less effective at quantifying drought stress in old large trees compared to physiologically focused measurements such as sap flow or stable isotopes (Fernandes et al., 2016; Keeling et al., 2011; McDowell et al., 2003; Simonin et al., 2007). Given the ecological importance and declining populations of large trees (Lutz et al., 2018; Lindenmayer et al., 2014), additional research into the physiological responses of large old trees to drought is needed.

Our results generally support the first-order expectation that reduced competition during drought increases tree growth response. More than a century of fire exclusion means that dry, fire-prone forests have a surplus of biomass which is not sustainable with ongoing aridification. Reducing competition through mechanical thinning can help increase tree growth resilience to drought, but our data indicate there are variable responses as a function of species and size. Our finding that prescribed fire had little influence on growth response may be an artifact of this being a first-entry burn after prolonged fire exclusion or it may be that the mechanism of competition reduction is less important than the amount of competition reduction. Either way, building system-level resilience to ongoing climate change in Sierran mixed-conifer forests will require density reduction and the restoration of regular surface fire.

CRedit authorship contribution statement

Harold S.J. Zald: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Chance C. Callahan:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Matthew D. Hurteau:** Conceptualization, Writing – review & editing, Funding acquisition. **Marissa J. Goodwin:** Investigation, Data curation, Writing – review & editing, Visualization. **Malcolm P. North:** Conceptualization, Writing – review & editing, Funding acquisition.

Data Statement

The data and code that support the findings of this study are openly available in "Data from: Tree growth responses to extreme drought after mechanical thinning and prescribed fire in a Sierra Nevada mixed-conifer forest, USA" at <https://doi.org/10.5061/dryad.wh70rxwq0>

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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