EFFECTS OF PRESCRIBED FIRE ON DROUGHT RESISTANCE AND RECOVERY IN MIXED CONIFER FORESTS OF LASSEN VOLCANIC NATIONAL PARK, CALIFORNIA

By

Zachary J. Wenderott

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Forestry, Watershed, and Wildland Sciences

Committee Membership

Dr. Rosemary Sherriff, Committee Chair

Dr. Phil van Mantgem, Committee Member

Dr. Harold Zald, Committee Member

Dr. Erin Kelly, Graduate Coordinator

May 2021

ABSTRACT

EFFECTS OF PRESCRIBED FIRE ON DROUGHT RESISTANCE AND RECOVERY IN MIXED CONIFER FORESTS OF LASSEN VOLCANIC NATIONAL PARK, CALIFORNIA

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Forests throughout much of the western United States are experiencing increasing climatic variability, often resulting in decreased forest productivity and elevated likelihood of tree mortality. Severe drought, such California's recent 2012-2015 drought, are projected to increase in intensity, frequency, and severity throughout much of this region in coming years. Forest management has long relied on prescribed fire and mechanical thinning to reduce fuel loads and ameliorate potential fire hazards. These treatments may also have the ability to reduce stand density, alleviate competitive pressures, and allow residual trees access to critical resources during periods of extreme stress. Utilizing a long-term National Park Service fire monitoring program allowed us to analyze the effects of prescribed fire treatments on radial growth response in a mixed-conifer forest of northern California.

Tree core samples were collected and analyzed from 136 yellow pine (ponderosa pine (*Pinus ponderosa)* and Jeffrey pine (*Pinus jeffreyi*)) and 136 white fir (*Abies concolor)* trees within Lassen Volcanic National Park. Tree-ring data was used to describe factors that influenced tree growth during the locally identified low moisture

period (2007 - 2015), as well the potential ability of treatments to improve tree drought resistance and subsequent recovery.

Radial growth was positively associated with crown ratio and annual precipitation totals, and negatively associated with localized competitive pressures. Within treatment sites, where stand density was effectively reduced, trees showed improved annual radial growth rates. This appeared to be generally driven by overall treatment intensity and its ability to alter forest density. White fir exhibited a stronger growth response to competitive pressures compared to yellow pine; however, radial growth rates were generally driven by the same factors. Drought resistance did not appear to be strongly correlated with competitive pressures, though drought recovery was slightly associated with increased competitive levels. Findings suggests future forest management techniques, such as prescribed fire and thinning, may be beneficial in terms of reducing competitive pressures and improving radial tree growth among residual trees during future more severe drought.

ACKNOWLEDGEMENTS

Funding for this project was provided through several resources including the United States Geological Survey (USGS), the National Park Service (NPS), and Humboldt State University (HSU). I would like to acknowledge and thank the members constituting my thesis committee, Rosemary Sherriff, Phillip van Mantgem, and Harold Zald. None of this could have been completed without field assistance from Alex Magliano, Christina Loria, and Niko Tutland. Thank you to Kelly Muth for lending her expertise in the HSU Dendrochronology Lab and to Micah Wright for his data analysis skills within R studio.

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INTRODUCTION

Climate-related weather extremes have been widely observed over recent years and have been largely attributed to global increases in surface air temperatures compared to pre-industrial levels (Wuebbles 2017). In the western United States, increasing air temperatures are driving an increase in atmospheric water demand, exacerbating periodic droughts (Williams et al. 2013). As temperatures rise, climate models predict greater variability in regional climate characteristics compared to historic levels (IPCC 2018), increases in the frequency and severity of drought and precipitation deficits (Adams et al. 2009; Dai 2013; Trenberth et al. 2014; Cook et al. 2015), and increases in volatility of such events (Swain et al. 2018). Forest ecosystems experiencing prolonged periods of abnormally low rainfall and available water resources are highly susceptible to drought-related tree stress (Williams et al. 2013), which can negatively affect forest composition, function, and productivity (Breshears et al. 2005; Allen et al. 2010; Phillips et al. 2010). While a reduction in available water may be the primary driver of drought-induced stress, higher temperatures can result in increased rates of evapotranspiration, reducing available water and intensifying drought stress on individual trees (Adams et al. 2009; Allen et al. 2015).

Trees subjected to drought-related stress often exhibit symptoms including wilting, foliage shedding, decreases in annual tree growth, and are at elevated risk of succumbing to mortality (Hanson and Weltzin 2000; Das et al. 2013; Crocket and We

sterling 2018). Furthermore, drought-stressed trees are more susceptible to insect attack, compounding the likelihood of mortality (Raffa et al. 2008; Anderegg et al. 2013; Anderegg et al. 2015; Fettig et al. 2019; Stephenson et al. 2019). Long-term moisture deficits, exceeding a single year, may lead to multi-year moisture overdraft as subsurface moisture levels are exhausted (Goulden and Bales 2019). These long-term deficits have been linked to increases in tree physiological stress and its accompanying effects (e.g., mortality) and places further emphasis on studies showing background tree mortality in the absence of fire is correlated with multi-year drought (Das et al. 2013). Additionally, observations in the Sierra Nevada show that moisture stress during the 2012 to 2016 drought were particularly acute in areas with dense vegetation (Goulden and Bales 2019). As future droughts are expected to be “hotter”, longer in duration and more intense, it is becoming imperative to prepare forests and increase the likelihood of continued growth and survival during these periods (Allen et al. 2015).

Fire suppression practices beginning in the 20th century throughout much of the western United States have resulted in the accumulation of forest fuels and increased present-day fire hazards (Stephens and Ruth 2005). Moreover, fire suppression has shifted many forest structures and species compositions (Lu et al. 2005; Stephens et al. 2009). The most profound effects have been seen in seasonally dry, low and mid-elevation coniferous forests that historically experienced frequent, low to moderate intensity fire regimes (Agee and Skinner 2005; Stephens et al. 2009). Fire suppression practices have increased fire return intervals throughout these areas which in turn has led

to elevated stand densities throughout a variety of forest types (Stephens 1998; Millar et al. 2007).

Many forests in which fire has been excluded now contain dense, slow-growing, shade-tolerant young trees (Skov et al. 2004) and declining numbers of large diameter trees (Lutz et al. 2009). Large diameter trees serve as important biological legacies (Parsons and DeBenedetti 1979), and comprise a large fraction of biomass within forests (Lutz et al. 2012; Stephenson et al. 2014) that influence rates and patterns of regeneration and succession (Keeton and Franklin 2004), as well as light, water accessibility, and other resources for smaller diameter trees (Binkley et al. 2010).

Forest structure has the ability to mediate the effects of drought-induced forest mortality because individual trees respond to drought differently depending on their competitive environment (Clark et al. 2014). Stand-level tree growth has been positively related to soil moisture availability which, even as temperatures rise, has been shown to be greatest in low density stands (Andrews et al. 2020). Several recent studies support that the effects of drought-related disturbances may be reduced with decreased stand density and alleviating competitive pressures on remaining individuals (Young et al. 2017; Tepley et al. 2020). Furthermore, elevated stand densities and local competitive pressures have been well documented as a contributing factor to individual tree mortality (Das et al. 2011; Gleason et al. 2017) and drought sensitivity (Voelker et al. 2018), suggesting a possible benefit of silvicultural thinning practices in terms of improving tree growth and likelihood of survival across drought stricken landscapes.

In an attempt to mitigate the effects of historic Euro-American land use practices while also restoring fire as a natural process, land management agencies primarily utilize two approaches to reduce the risk of future severe fire events: 1) mechanical thinning to remove low to mid-canopy trees and reduce local basal area; and 2) prescribed fire to reduce ground and ladder fuels and remove small diameter trees (Stephens and Ruth 2005). Recently, management goals have expanded to consider ecological resilience to expected future increases in disturbance (such as drought) frequency and intensity (Millar and Stephenson 2015). Ecological resilience is defined as the ability of a system to absorb impacts before a threshold is reached where the system changes into a different state and alters overall forest health (Gunderson 2000; Falk et al. 2019). Determining if current fire management activities enhance forest resistance (ability to remain unchanged during disturbance events) and subsequent recovery (ability to return to pre-disturbance growth rates) (Lloret et al. 2011) to drought is essential for maintaining future forest structure. Additionally, prescribed fire may provide a more economically viable means of addressing fire deficits compared to mechanical thinning (North et al. 2012, North et al 2015).

Reducing forest density may increase the productivity of remaining trees by allowing them access to critical resources while also alleviating the vulnerability to future wildfire and pathogen attacks (Latham and Tappeiner 2002). A recent study in a dry, mixed-conifer forest of northern California found that mechanical thinning treatments effectively reduced competitive pressures and increased residual tree growth during the recent severe drought in California (Vernon et al. 2018). This study supports other

findings that illustrate thinning treatments can enhance long-term average growth throughout high and low temperature periods (Andrews et al. 2020) and may improve tree growth-rates and stand resilience under drought conditions (Thomas and Waring 2015). Likewise, prescribed fire can also reduce stand density and may improve the likelihood of tree survival throughout periods of drought (van Mantgem et al. 2016). Enhanced carbon assimilation during late-season climatic stress was found to be associated with prescribed fire treatments suggesting additional benefits during periods of climatic stress (Tepley et al. 2020). However, tree mortality rates may increase with prescribed fire treatments immediately prior to the onset of severe drought (Knapp et al. 2020) and/or increase the rate of bark beetle infestation (Steel et al. 2020).

The recent California drought (2012-2015) was among the most extreme droughts in California's recorded history (Robeson 2015; Williams et al. 2015), and likely among the most severe in the past 1,200 years within this region (Griffin and Anchukaitis 2014). Using this event as a natural experiment, I quantified the effects of an ongoing National Park Service (NPS) prescribed fire program in Lassen Volcanic National Park, California to improve overall tree-growth response to this period of low precipitation. Specifically, this study will address the following questions: 1) What factors (prescribed fire history, competition, precipitation, and tree characteristics) influence white fir (*Abies concolor*) and yellow pine (*Pinus* spp.) radial tree growth? 2) Are prescribed fire treatments effective in reducing local competition and increasing tree-growth response? And 3) how do local competition and prescribed fire treatments effect resistance (ability to maintain pre-disturbance radial growth rates) and recovery (the ability of a tree to return to pre-

disturbance radial growth rates) at the immediate (1-2 years) cessation of multi-year low precipitation events?

MATERIALS AND METHODS

Study Area

This study was conducted in two mixed-conifer forest sites within Lassen Volcanic National Park (LAVO), located at the southern tip of the Cascade Mountain Range, approximately 76 km east of Redding, California. The climate of LAVO is described as Mediterranean, characterized by cold, wet winters and warm, dry summers (Taylor 1995). Average annual total precipitation within this area is 105 cm, of which approximately seven percent falls during summer months (July to September). The average annual snowfall is nearly 450 cm (Davey et al. 2007). Throughout winter months, average daily temperature is 0 °C, with average lows of -6 °C. Average temperature during summer months is 15 °C and average daily maximum is 24 °C (Western Regional Climate Center 2019).

Annual precipitation throughout the duration of the study period ranged from 1701.5 mm (high) to 437.0 mm (low). The 30-year average (1988 – 2017) was 889.4 mm and average precipitation during drought (2007 – 2015) was 630.4 mm. All weather data for the study was obtained from the Manzanita Lake weather station (1783 m), located just outside the western boundary of LAVO, representing a similar geographic area as that in which the study was carried out (Figure 1).

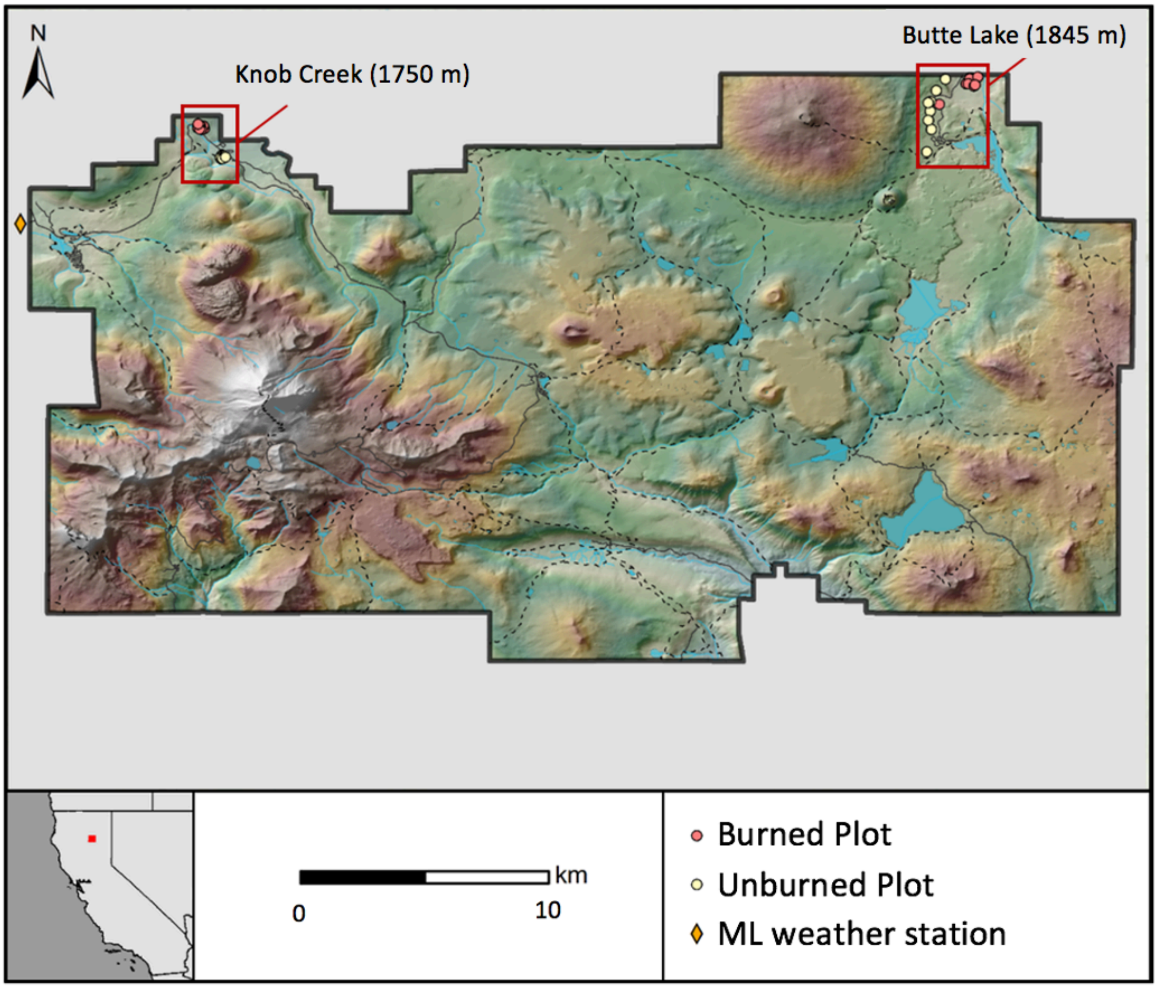

Figure 1. Knob Creek and Butte Lake study sites in relation to Manzanita Lake (ML) weather station within Lassen Volcanic National Park in northern California. Map color represents elevational gradient and water bodies.

In the early 1850's, near what would later become the northern boundary of LAVO, the Nobles Emigrant Trail was established as an alternative route through northern California for gold prospecting expeditions and westward Euro-American expansion (White 2016). The resulting land-use activities, such as livestock grazing and intensive timber harvest, and the influx of settlers had lasting effects on the structure of

the forests throughout this region (Miller and Safford 2017). Pre-settlement conditions in mixed-conifer forests of the southern Cascade mountain range supported fire regimes characterized by frequent, low to moderate-severity fires with fire return intervals of approximately 5-14 years (Bekker and Taylor 2001).

Originally designated as a national monument in 1907, it was not until subsequent volcanic activity in 1914 that the park would garner enough national attention to be designated as a National Park (1916). LAVO encompasses approximately 43,000 hectares of forests, meadows, and shrublands (31,000 hectares designated as wilderness). LAVO is bound by three distinct biological provinces: the Sierra Nevada Mountain Range to the south, the Cascade Mountain Range to the north, and the deserts of the Great Basin to the east (NPS 2019). Variations in environmental factors such as elevational gradients (1,524 to 3,187 m), total precipitation (75 cm in eastern portions to 300 cm at high elevations), and seasonal temperature give rise to diverse and abundant flora and fauna within LAVO (NPS 2019).

Study Sites

Two field sites were established within LAVO: Butte Lake (elevation 1845 m), located in the northeastern portion of LAVO and Knob Creek (elevation 1750 m), approximately 18 km west of Butte Lake (**Error! Reference source not found.**). Within sample locations, the forest canopy is primarily dominated by ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*) mixed with more shade tolerant white fir (*Abies concolor)* and occasional sugar pine (*Pinus lambertiana*) and incense cedar

(*Calocedrus decurrens*). Collectively, Jeffrey pine and ponderosa pine were sampled as yellow pine (PIXX) due to difficulty in field identification of young individuals, as well as an overlap in species distribution and potential hybridization throughout this region (Critchfield 1975). Understory species primarily consisted of manzanita (*Arctostaphylos spp.*), gooseberry (*Ribes spp.*), and tobacco-brush (*Ceanothus velutinus*) (NPS 2019).

Soil types within the Knob Creek and Butte Lake field sites are categorized as humic haploxerands and ashy sand, respectively, both of which are derived from volcanic rock and are typically described as well drained soils (USDA 2010). Available water storage is similar among all sampled plots and soils are categorized as drought-vulnerable (Soil Survey Staff 2019).

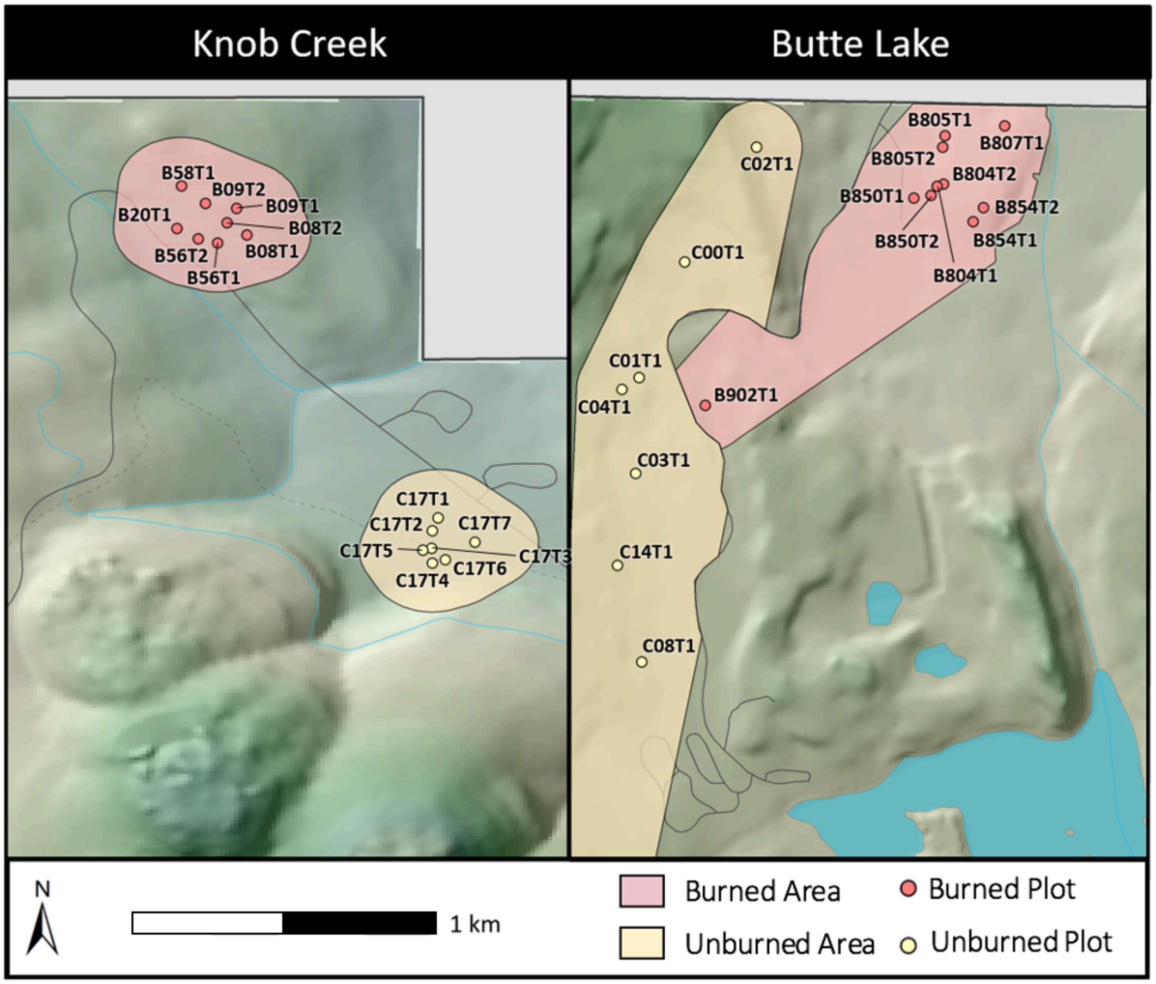

Figure 2. Site location for burned and unburned plots sampled at Knob Creek and Butte Lake within LAVO.

The Butte Lake and Knob Creek sites are part of a long-term National Park Service (NPS) prescribed fire management program (FMH) (USDI 1992) aimed at reducing local fuels loads and decreasing the likelihood of potential stand-replacing fire events. FMH plots were installed at random locations and random orientations within individual burn sites prior to treatment (USDI 2003, see page 67 in FMH protocols). Within FMH plots, all live trees > 15 cm DBH (diameter at breast height, 1.37 m above

ground) trees were tagged, identified to species, assessed as living/dead, and measured for stem diameter prior to fire and typically immediately post-fire, 1-, 2-, 5-, 10-yr post-fire, and at 10-yr intervals thereafter.

All sampled burned plots were established in 1993 with the exception of three Butte Lake plots (B804, B805, B902; est. 1990) and a single plot within the Knob Creek sample area (B09; est. 1992). Within Butte Lake, initial prescribed fire treatments were applied in 1995 with the exception of a single plot (B902; treated 1990). All treated plots within Butte Lake underwent a secondary burn treatment in 2004. Within the Knob Creek sample site, all plots received a single prescribed burn treatment in 1993. Long-term fire effects data has been periodically collected, including pre-treatment data, and allowed for quantification of fire severity (char height) as well as estimates of changes in forest density and basal area as a product of treatment.

Study Design

In 2018, eighteen (Butte Lake, *n* = 10; Knob Creek, *n* = 8) temporary burned transects were established using pre-existing FMH plot corners as a point of origin. Each FMH plot was marked with tagged rebar upon initial installment assuring correct establishment of temporary plot location for sample collection. From the marked rebar, a 50-meter transect was established parallel to the FMH plot orientation and projecting away from the existing plot. Only trees located outside of the FMH plots were sampled in an attempt to minimize disruption of these long-term monitoring plots.

Fifteen (Butte Lake, *n* =8; Knob Creek, *n* =7) unburned (control) transects were established using randomly generated points selected for similar elevation, species composition, slope (restricted to <30% slope), aspect (similar to burn sites), ease of access, and general proximity to burned transect locations. A 50-meter buffer zone excluded all streams, roads, trails, and wilderness areas from potential sampling. A point of origin was marked with a pin flag (removed at the end of the measurement) for the temporary plot locations. From this point, a 50-meter transect line was placed in a randomly selected azimuth.

For all transects (burned and unburned), ABCO and PIXX were sampled at 10 m, 30 m, and 50 m points on the transect line. At each point location, the nearest two individuals >30 cm DBH and within 20 m of the transect line were sampled (Figure 3), allowing a maximum of 12 trees (6 ABCO and 6 PIXX) to potentially be sampled from each transect. Sampling design allowed for potential overlap of trees at consecutive sampling points. In this circumstance, the previously sampled tree was omitted, and the next nearest tree was sampled. Trees exhibiting severe deformities (e.g., fused stems, broken top) or extreme pathogen attack were excluded from sampling entirely. If necessary, this process was repeated at another corner of the FMH plot to ensure a relatively equal distribution between sampled species.

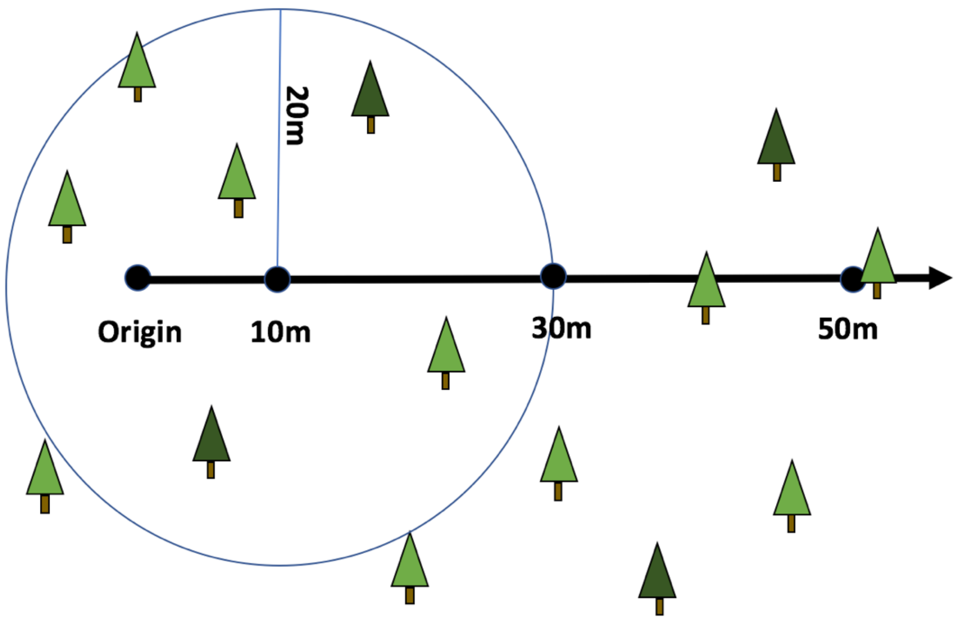

Figure 3. Layout of hypothetical temporary burn and unburned sampling transects. Each color represents a unique tree species.

Field Sampling

566 tree core samples (2 cores per individual) were extracted from 283 selected trees (ABCO, *n* = 138; PIXX, *n* = 145). One increment core was extracted approximately 50 cm above ground level, perpendicular to the proximal slope; a secondary core was collected from the opposite side of the tree. Height of extraction, depth of core, and diameter of tree at core extraction height were also collected. For each cored tree I collected species identity (ABCO or PIXX), stem DBH, compacted crown ratio (ocular estimate of percent total tree stem length supporting live foliage), tree canopy position, maximum stem char height (used as a metric of fire severity) and other tree damage

conditions (presence/absence of pathogens, bole scars, or rot). Any other relevant information pertaining to the health of the individual tree was recorded.

A 10 m fixed-radius plot was established around each focal (cored) tree to assess local competitive pressures. At each focal tree, all competitor trees > 5 cm DBH were included. Species identity, DBH, and distance from the focal tree were recorded.

Laboratory Methods

Core Preparation

Tree cores were air dried, mounted and sanded using progressively finer grit sandpaper following standard dendrochronological processing methods (Pilcher 1990). Hand polished cores were mounted and scanned at 1200 resolution dpi (dots per inch). The computer software WinDENDRO (Reg 2014a; Regent Instruments Inc. Quebec, Canada) was used to detect and measure annual growth rings to the nearest 0.001 mm accuracy. The computer program COFECHA was used to cross-date tree-ring series by checking measured tree-ring series for correlation (Holmes 1983). Only tree cores that were confidently cross-dated were used for further statistical analysis. If two core samples were collected for an individual tree, the annual growth measurements for each year were averaged across the pair. If one (or both) of the cores collected were of poor quality (rot, missing segments, suppressed/unreadable rings, etc.), they were excluded from further analysis. These criteria removed 11 trees (ABCO, $n = 2$; PIXX, $n = 9$) and reduced the total number of trees suitable for further analysis to 272 (ABCO, $n = 136$; PIXX, $n = 136$).

Tree Growth Response

Basal area increment (BAI) is a widely used measurement of wood produced by individual trees during a single growing season (LeBlanc 1990; Biondi and Qeadan 2008). Raw ring-width series were converted to annual tree BAI (cm^2 yr^{-1}) using diameter of tree inside bark at coring height. BAI is less dependent on tree diameter and avoids the need for detrending methods (Biondi 1999), which can remove low-frequency variability and may produce larger errors towards the inner portion of the tree-ring chronology (Kohler et al. 2010). This conversion allows for better representation of annual wood production of individuals with different width-diameters. Bark thickness (BT) was calculated using the following allometric regression equation derived from trees sampled in the Klamath National Forest in northern California (Zeibig-Kichas et al. 2016):

1) White fir (ABCO) $\sqrt{BT} = 1.005 * \sqrt{DBH}^{0.856}$

2) Ponderosa/Jeffrey pine (PIXX) $\sqrt{BT} = 1.298 * \sqrt{DBH}^{0.802}$

where DBH is the diameter of tree outside bark at coring height. Tree radius inside bark was estimated by subtracting BT from tree radius at coring height. Subsequently, the width of each ring was calculated starting from the outermost growth ring and subtracting each additional measurement towards the pith using the dplR package (Bunn 2008) in the R statistical software (R Core Team 2018) which then converts these measurements to annual BAI.

Competition Metrics

The Hegyi index (HI) was used to quantify the influence of competition on the growth of focal trees (Hegyi 1974). HI is a unitless metric that assumes the DBH (of both focal tree and competitor tree) and distance between the focal tree and competitor trees reflect their overall competitive interaction (Das et al. 2008; van Mantgem and Das 2014). This metric was calculated using the following equation:

$$HI = \sum_{j \neq i} \frac{DBH_j}{DBH_i \times (Dist_{ij} + 1)} \quad (3)$$

where DBH_i is the diameter (cm) of the focal tree, DBH_j is the diameter (cm) of the neighboring tree, and $Dist_{ij}$ is the distance (m) between the focal tree and the neighboring tree. Competition from all neighboring trees (> 5 cm DBH) within a fixed 10-meter radius of the focal tree was calculated and summed to create a distant-dependent value representing relative competitive pressures subjected to each focal tree.

Climate Data

Daily climate data from the Manzanita Lake Weather Station (located approximately 10 km southwest of Knob Creek and 22 km west-southwest of Butte Lake field sites) for the period of 1970-2017 was obtained from the Western Regional Climate Center (WRCC 2019). All missing entries (8.1/year or approximately 2.2% total) were interpolated from recorded values based on the local 5-day rolling mean. Daily minimum

and maximum temperatures (˚C) were used to calculate mean daily temperature throughout the duration of the study. Monthly precipitation totals were calculated and summed to the water year (October – September) to create yearly precipitation totals. In this study, I explored an improved form of the Palmer Drought Severity Index (PDSI) known as the self-calibrating Palmer Drought Severity Index (scPDSI) (van der Schrier et al. 2013) which utilizes soil moisture availability and has been used as an effective indicator of long-term droughts. The packaged 'scPDSI' (Zhong et al. 2018) was used to calculate monthly conventional and self-calibrating PDSI using precipitation and monthly potential evapotranspiration (PET). PET was calculated using the Thornthwaite equation (Thornthwaite 1948). For all scPDSI calculations a default of 100 mm available water content (AWC) was used.

During analysis, tree growth was more closely correlated with annual precipitation totals than with scPDSI. For the sake of simplicity, I continued data analysis using precipitation totals obtained from Manzanita Lake weather station. The locally sourced climate data was ground-truthed against the gridded surface meteorological data set from the University of Idaho (gridMET) to assure accuracy (Figure 4). The period of low rainfall (2007 – 2015) was selected using 1 standard deviation from the 30-year (1988 – 2017) mean as a guideline.

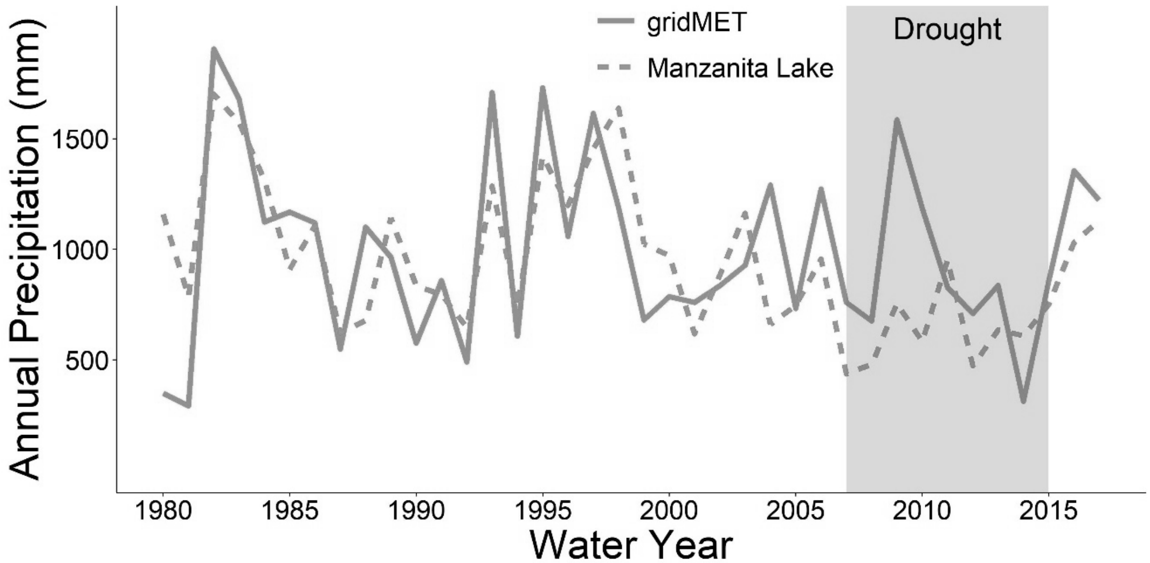

Figure 4. Comparison of annual precipitation values (mm) for data obtained from Manzanita Lake weather station (dashed line) and gridMET (solid line). Water year is defined as (October – September). Data from Manzanita Lake was ultimately used for analysis. Gray area indicates the onset and duration of drought.

<u>Drought Resistance and Recovery Metrics</u>

To assess tree response to the most recent drought in this region, drought resistance (DrResist) and recovery (DrRecov) metrics were created for each tree sampled. These metrics were calculated using the following equations:

4) $$DrResist = DurDr/PreDr$$

5) $$DrRecov = PostDr/DurDr$$

where DurDr is the mean annual BAI for the 9 years during drought (2007 – 2015), PreDr is mean annual BAI for the 9 years prior to the onset of drought (1998 – 2006), and

PostDr are the two years immediately following drought (2016-2017) (Lloret et al. 2011). Using equation (4), values greater than 1 indicate improved growth during drought (high drought resistance) and values less than 1 indicate reductions in growth during drought (low drought resistance). Using equation (5), values greater than 1 indicate improved growth immediately following drought (high drought recovery), and values less than 1 indicate reductions in growth following the drought (low drought recovery).

Statistical Analysis

To determine the effects of precipitation on white fir and yellow pine annual BAI, I used annual water-year precipitation totals from 1970 – 2018 (selected to include complete tree-ring data for all sampled trees) collected at Manzanita Lake weather station. Current year, 2-year, and 3-year rolling mean precipitation totals were explored to account for potential lag effects of precipitation effects. Species-specific generalized linear mixed-effects models (GLMM, gamma distributed with an inverse link) were created using yearly BAI as the response variable (n = 6,664, 136 focal trees with 49 observations per individual). A temporal model builder was included using the glmmTMB package within R (Magnusson et al. 2017) to create a first-order autocorrelation term to account for serial correlations in annual growth among years within individual trees. Models included a nested random effect of individual tree within plot to account for variation between site condition and individuals using the process previously described. Models within 2 AIC units of the lowest model were considered for

final analysis. Differences in treatment and species effects were also explored by creating and comparing estimated bootstrapped confidence intervals based on 1000 samples.

I evaluated the primary factors influencing individual radial tree growth and the effects of treatment by creating species-specific GLMM's (gamma distributed with an inverse link) using an average of the 10 most recent years (2008-2017) of BAI as the response variable (n = 1360, 136 focal trees with 10 observations per individual; the same total for each species-specific model). Both species-specific models included random effects of plot to help address unaccounted variation in site condition.

Drought resistance and recovery metrics previously described were used to assess the effects of treatment on white fir and yellow pine radial growth during the period of low rainfall observed and the immediate years following. GLMM's were created to test the effects of species, treatment, crown ratio, and competition on both drought resistance and recovery (both Gaussian distributed). Models included a random effect of plot to account for variation between sites.

To determine random effects, I created a series of statistical models with a variety of combinations of random variables and utilized the Akaike Information Criteria (AIC) to select the simplest model with the most explanatory power (Zuur et al. 2009). A series of GLMM's with different explanatory variables, including interaction terms, were fitted and compared using AIC. All final models were selected based on the lowest AIC value and residuals were checked to ensure homoscedasticity. Marginal and conditional r^2 values were calculated using the r.squaredGLMM function of the MuMIn (Bartoń 2016) package to help explain the variance provided by the fixed effects. Current software does

not support calculation of marginal and conditional r^2 values for models including an autoregressive term. In this circumstance, a pseudo-r^2 was calculated. The value set to determine the level of significance for all analysis was $\alpha = 0.05$.

RESULTS

Plot-level Responses

Within the Butte Lake collection site, prescribed fire treatments reduced average stem density from 371.7 trees ha^{-1} prior to treatment to 143.3 trees ha^{-1} (61.4% decrease) five years after first-entry burn and further reduced to 116.7 trees ha^{-1} (additional 18.6% decrease) five years post second-entry burn (Figure 5). Pre-burn average basal area within Butte Lake was reduced from 46.7 m^2 ha^{-1} to 32.8 m^2 ha^{-1} (29.8% decrease) and 32.5 m^2 ha^{-1} (additional 0.01% decrease) after first and second treatments, respectively. Average stem density at the Knob Creek site was 436.0 trees ha^{-1} prior to treatment and reduced to 374.0 trees ha^{-1} (14.3% decrease) five years after the first and only prescribed burn. Average basal area at Knob Creek was only slightly reduced, decreasing from 56.9 m^2 ha^{-1} prior to treatment to 50.9 m^2 ha^{-1} (10.5% decrease) five years post treatment (Figure 5). By 2018, stand basal area at Knob Creek had returned to similar levels of those prior to prescription treatments.

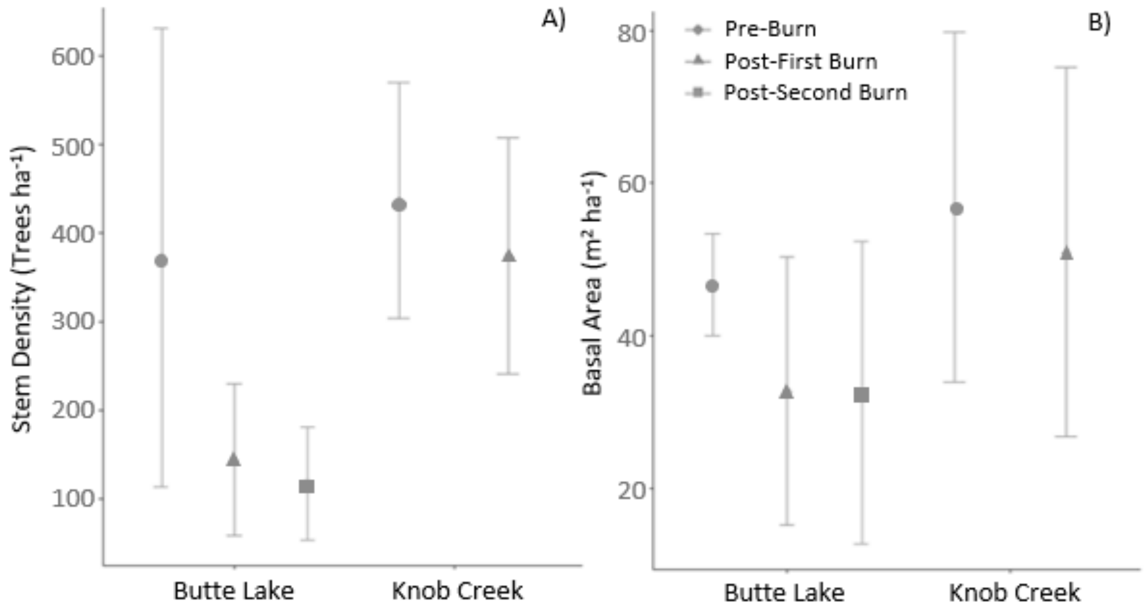

Figure 5. Changes in mean (± 1 SD) plot-level stem density (A) and mean basal area (B) from pre-burn (circle) conditions to 5-years post first-entry burn (triangle) and 5-years post second-entry burn (square) at Butte Lake (10 plots) and Knob Creek (8 plots) burn sites within LAVO. Note the different y-axis scales between stem density and basal area.

Tree and Stand Conditions

Mean focal tree DBH was similar between burned and unburned sites and species with the exception of PIXX sampled at unburned Knob Creek sites that generally had a slightly higher DBH. Average crown ratio was consistently higher in trees subjected to treatments across both species and locations. HI was lower for both species sampled in Butte Lake burned versus unburned sites, however, HI was higher for both species in burned sites at Knob Creek (Table 1).

Table 1. Summary statistics for yellow pine (PIXX) and white fir (ABCO) individuals sampled within burned and unburned sites at Butte Lake (BL) and Knob Creek (KC) sites in Lassen Volcanic National Park. Average values (± 1 standard deviation) are shown for focal tree diameter at breast height (DBH), percent crown ratio, and Hegyi competition index (HI).

Species	**Site**	**Outcome**	**# Focal Trees**	**Focal DBH (cm)**	**Crown Ratio (%)**	**HI**
PIXX	BL	Burned	43	72.7 ± 28.1	46.8 ± 12.4	0.44 ± 0.42
PIXX	BL	Unburned	40	66.6 ± 24.3	44.7 ± 12.0	0.88 ± 0.56
ABCO	BL	Burned	37	62.9 ± 24.5	61.6 ± 11.0	0.64 ± 0.57
ABCO	BL	Unburned	37	58.5 ± 27.3	58.6 ± 13.6	1.31 ± 0.78
PIXX	KC	Burned	26	69.4 ± 26.1	46.5 ± 14.5	1.21 ± 1.27
PIXX	KC	Unburned	29	85.1 ± 18.6	38.7 ± 10.9	0.75 ± 0.46
ABCO	KC	Burned	30	45.7 ± 13.1	50.1 ± 17.4	2.09 ± 0.99
ABCO	KC	Unburned	30	47.1 ± 20.6	46.8 ± 15.5	1.99 ± 1.08

Influence of Precipitation on Radial Tree Growth

Annual precipitation had a significant positive effect on mean annual BAI for both yellow pine and white fir (Table 2-Table 3). In general, yellow pine showed a slightly stronger response to precipitation than white fir. Yellow pine exhibited a greater relationship with two-year precipitation average compared to current year precipitation in white fir (Figure 6). Predicted values for white fir and yellow pine show that the models explained a substantial amount of variation within BAI (white fir pseudo-r^2 = 0.85, yellow pine pseudo-r^2 = 0.80).

Table 2. Top generalized linear mixed-effects models for basal area increment from 1970-2017 for yellow pine (PIXX) and white fir (ABCO). Final model includes predictor for mean 2-year annual precipitation (PPT2) and current year precipitation total (PPT). An intercept-only model with no fixed effect predictor variables is also shown.

Model	Predictors	df	logLik	AICc	ΔlogLik	ΔAICc
PIXX	PPT2	9	-17850.9	35719.8	73.3	0.0
	intercept only	8	-17924.2	35864.5	0.0	144.7
ABCO	PPT	9	-18353.6	36725.2	67.5	0.0
	intercept only	8	-18421.1	36858.2	0.0	133.0

Table 3. Parameter estimates and variation for the top generalized linear mixed-effect models of yellow pine (PIXX) and white fir (ABCO) for basal area increments from 1970-2017. Model parameters include mean 2-year annual precipitation for yellow pine (PPT2) and current year precipitation totals for white fir (PPT). Parameter 95% confidence intervals (CI) estimated from 1000 bootstrapped samples.

Model	Term	Estimate	CI
PIXX	PPT2	0.15	0.13 to 0.16
ABCO	PPT	0.10	0.09 to 0.11

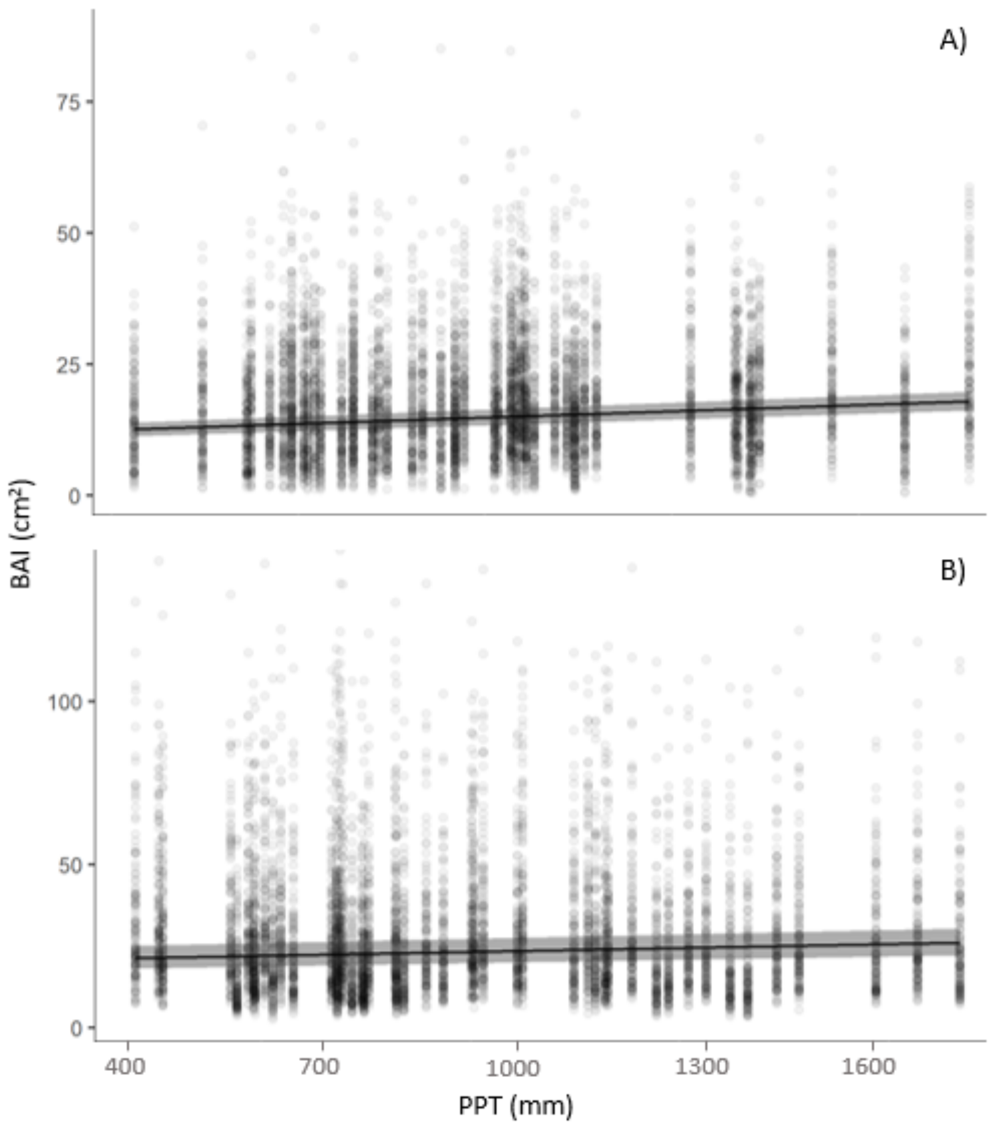

Figure 6. Basal area increments (BAI) and precipitation (PPT) from 1970-2017 for yellow pine (PIXX) (A) and white fir (ABCO) (B). Model predictors included yearly precipitation totals for white fir and mean 2-year annual precipitation for yellow pine. Note the different scale of the y-axis.

Among burned plots, white fir BAI appeared to have an increasing trend, including during the defined drought. However, BAI remained relatively constant for both species in unburned plots and yellow pine sampled in burned plots (Figure 7).

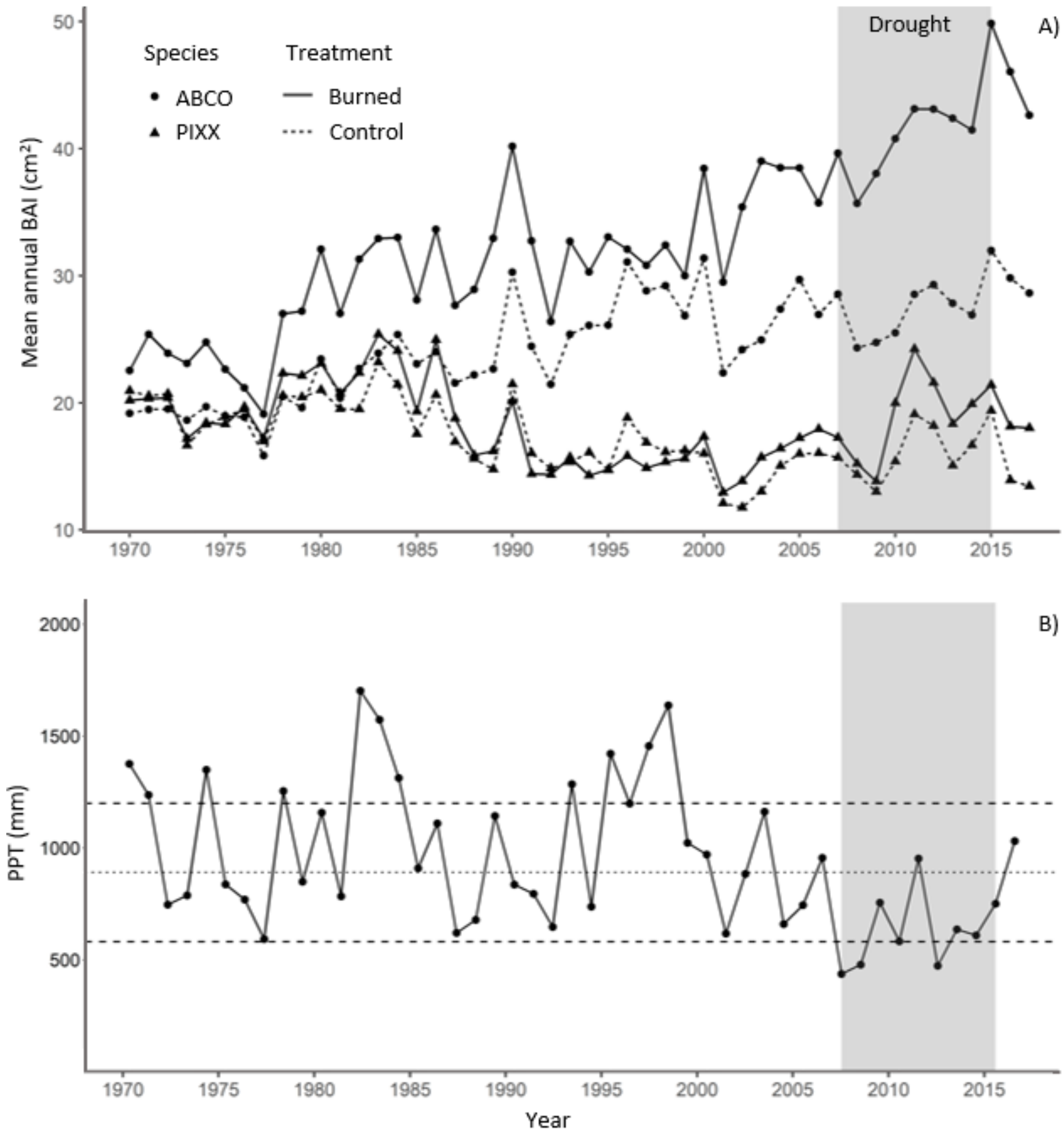

Figure 7. Time series (1970-2017) showing mean annual basal area increment (BAI) for yellow pine (PIXX) and white fir (ABCO) in burned (solid line) and unburned (dashed line) locations (A). Annual precipitation totals (PPT) recorded at the Manzanita Lake weather station (B). A horizontal dotted line represents the 30-year mean annual precipitation from 1988 – 2017 and horizontal dashed lines represent 1 standard deviation from the 30-year mean. Gray area indicates the onset and duration of drought, refer to text for definition.

Influences on Radial Tree Growth

The HI and percent crown ratio had significant effects on mean BAI (2008-2017) of both yellow pine and white fir (**Error! Reference source not found.**). For white fir, BAI was also influenced by treatment and an interaction between competition and percent crown ratio (Table 4).

Table 4. Top generalized linear mixed-effects models for growth from 2008-2017 for yellow pine (PIXX) and white fir (ABCO). Model predictors include percent crown ratio (CR), Hegyi competition index (HI), and treatment.

Model	Predictors	df	logLik	AICc	ΔlogLik	ΔAICc
PIXX	HI, CR	5	-484.0	978.4	4.6	0.0
	HI, CR, Treatment	6	-482.9	978.5	5.7	0.1
	Treatment, HI*CR	7	-482.4	979.6	6.2	1.2
	HI	4	-488.6	985.4	0.0	7.0
ABCO	Treatment, HI*CR	7	-504.8	1024.5	12.5	0.0
	HI, CR, Treatment	6	-507.9	1028.5	9.4	4.0
	HI*CR	6	-511.3	1035.4	6.0	10.8
	HI, CR	5	-513.6	1037.6	3.7	13.1
	HI	4	-517.3	1043.0	0.0	18.5

Model results indicated that yellow pine and white fir both exhibited greater BAI in individuals with higher crown ratios (Table 5, Figure 8). Competition was negatively associated with annual radial growth in both species, particularly in white fir (Figure 9). White fir in unburned sites exhibited a lower growth rate with a positive interactive effect

of competition and crown ratio (Figure 10). Final models for both species included a random intercept of plot which slightly improved the final white fir model (marginal r^2 = 0.64 and conditional r^2 = 0.71) but had no effect on the final yellow pine model (marginal r^2 = 0.17 and conditional r^2 = 0.17). However, I opted to retain the random effect in this scenario as the AICc value was still within 2 units of the model in which the random effect was omitted.

Table 5. Standardized parameter estimates and variation for the top generalized linear mixed-effect models of yellow pine (PIXX) and white fir (ABCO) growth from 2008-2017. Model parameters include percent live crown ratio (CR), Hegyi competition index (HI), treatment, and an interaction term. Parameter 95% confidence intervals (CI) estimated from 1000 bootstrapped samples are shown.

Model	**Term**	**Estimate**	**CI**
PIXX	HI	-0.33	-0.49 to -0.15
	CR	0.32	0.14 to 0.50
ABCO	HI	-0.70	-0.89 to -0.54
	CR	0.27	0.06 to 0.47
	Unburned	-0.32	-0.51 to -0.16
	HI*CR	-0.33	-0.50 to -0.16

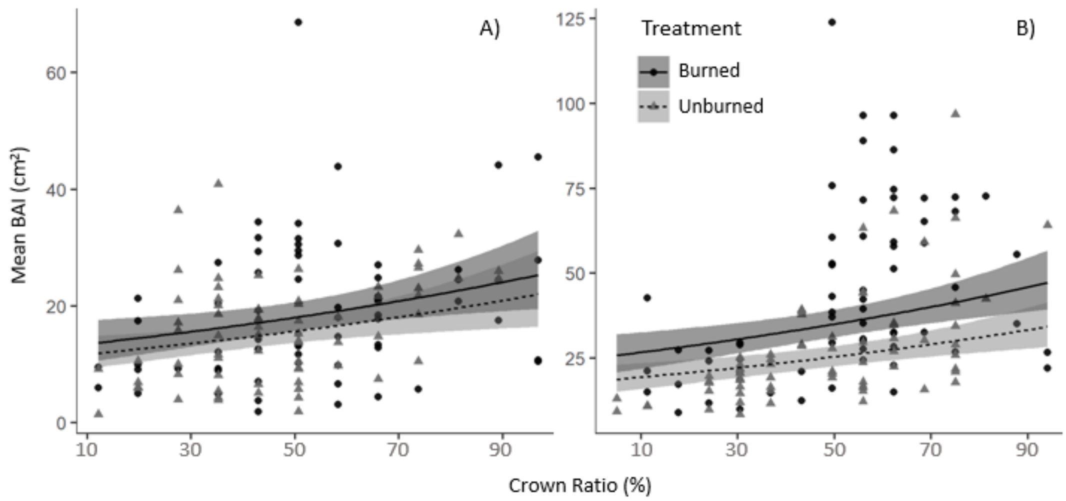

Figure 8. Estimated effects of crown ratio on mean basal area increment (BAI) from 2008-2017 with a 95% confidence interval for yellow pine (A) and white fir (B) from generalized linear mixed-effect models in burned (solid) and unburned (dashed) sample sites. Symbols represent observed data. Note the different y-axis scales between yellow pine and white fir.

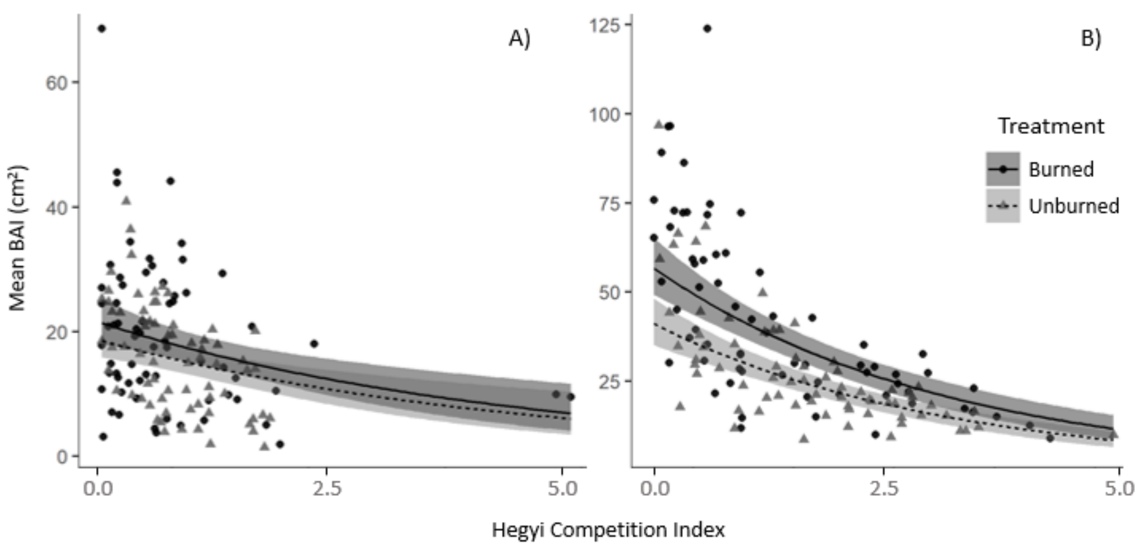

Figure 9. Estimated effects of competition index on mean basal area increment (BAI) from 2008-2017 with a 95% confidence interval for yellow pine (A) and white fir (B) from generalized linear mixed-effect models in burned (solid) and unburned (dashed) sample sites. Note the different y-axis scales between yellow pine and white fir.

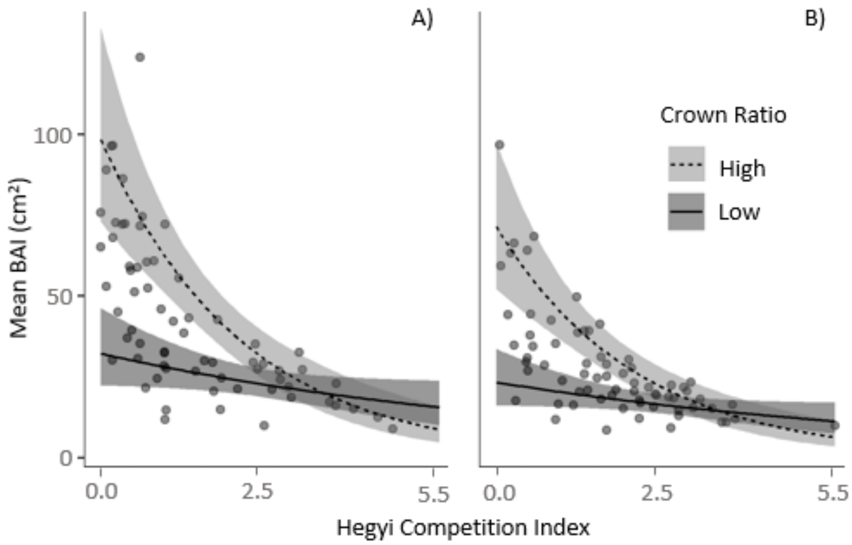

Figure 10. Estimated interactive effects of maximum (high) and minimum (low) levels of crown ratio and competitive pressures on mean basal area increment (BAI) from 2008-2017 for white fir with a 95% confidence interval from generalized linear mixed-effect models in burned (A) and unburned (B) sample sites.

Drought Resistance and Recovery

Drought resistance and recovery were most strongly associated with species and competition, and, in the case of drought recovery, crown ratio (Table 6). In general, yellow pine had slightly higher drought resistance and lower drought recovery compared to white fir, although only statistically significant in the case of drought recovery. Trees in higher competitive environments or with higher crown ratios showed increased drought recovery while neither factor proved to significantly influence drought resistance (Table 7; Figure 11). Final models for drought resistance and drought recovery explained a relatively low amount of variability (marginal r^2 = 0.01 and r^2 = 0.21, respectively).

However, the inclusion of a random intercept of plot slightly improved the final models (conditional $r^2 = 0.19$ and $r^2 = 0.24$, respectively).

Table 6. Top generalized linear mixed-effects models for DrResist (drought resistance) and DrRecov (drought recovery). Model predictors include species, crown ratio (CR) and Hegyi competition index (HI).

Model	Predictors	df	logLik	AICc	ΔlogLik	ΔAICc
DrResist	Species	4	-207.7	423.5	0.0	0.0
	Species, CR	5	-207.6	425.4	0.1	1.9
	Species, HI	5	-207.7	425.5	0.0	2.0
	Species, CR, HI	6	-207.6	427.5	0.1	4.0
	Species, CR*HI	7	-206.6	427.6	1.1	4.1
DrRecov	Species, CR, HI	6	31.0	-49.8	7.8	0.0
	Species, CR*HI	7	31.2	-48.1	8	1.7
	Species, HI	5	26.7	-43.2	3.5	6.6
	Species, CR	5	24.4	-38.6	1.2	11.2
	Species	4	23.2	-38.3	0.0	11.5

Table 7. Parameter estimates and variation for the top generalized linear mixed-effect models for drought resistance (DrResist) and recovery (DrRecov). Model parameters include species, treatment, Hegyi competition index (HI), and crown ratio (CR). Parameter 95% confidence intervals (CI) estimated from 1000 bootstrap samples and standard error (SE) are shown.

Model	Term	Estimate	CI
DrResist	Species (PIXX)	0.09	-0.02 to 0.19
	HI	0.00	-0.03 to 0.04
DrRecov	Species (PIXX)	-0.12	-0.20 to -0.06
	CR	0.05	0.02 to 0.07
	HI	0.06	0.02 to 0.10

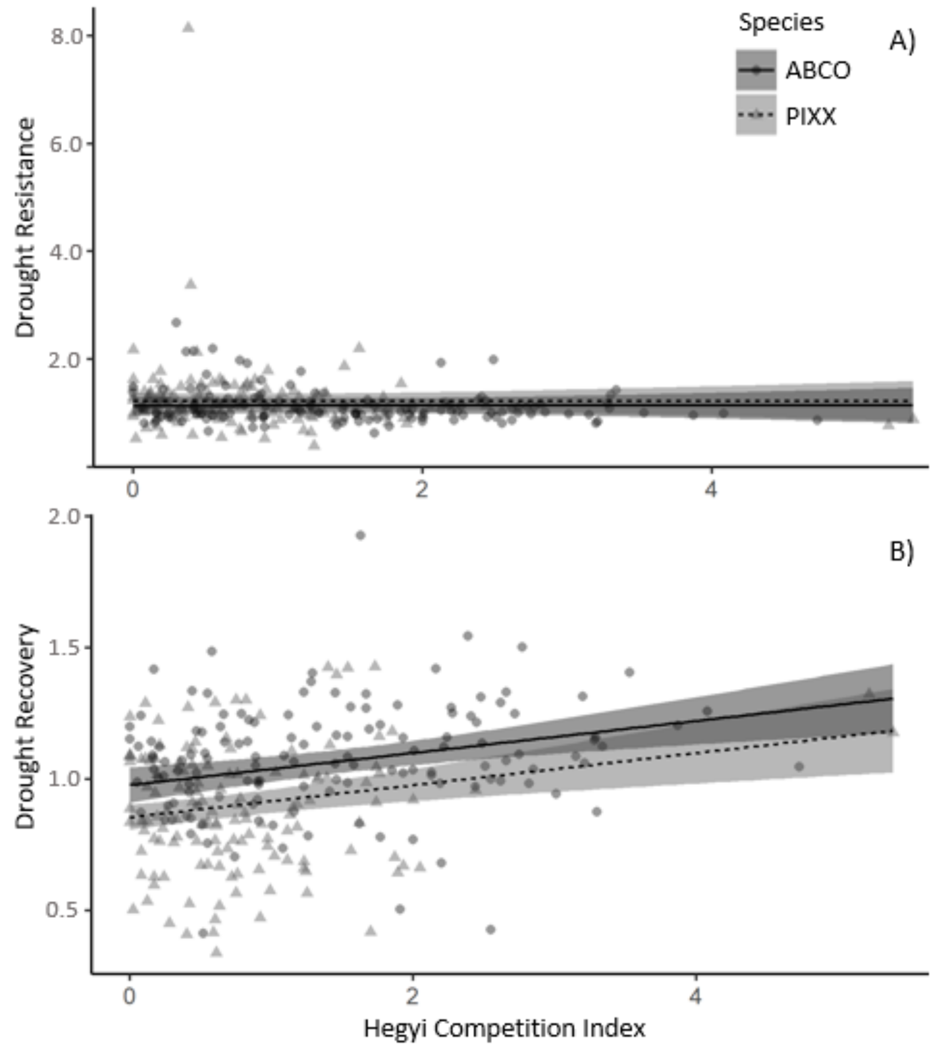

Figure 11. Drought resistance (A) and drought recovery (B) and Hegyi competition index (HI) for white fir (ABCO) and yellow pine (PIXX). Model predictors include species, HI, and, in the case of drought recovery, crown ratio. Note the different y-axis scales.

Mean drought resistance was relatively similar between treatments and species, although mean drought recovery was slightly higher in white fir, and in burned compared to unburned sites (Figure 12).

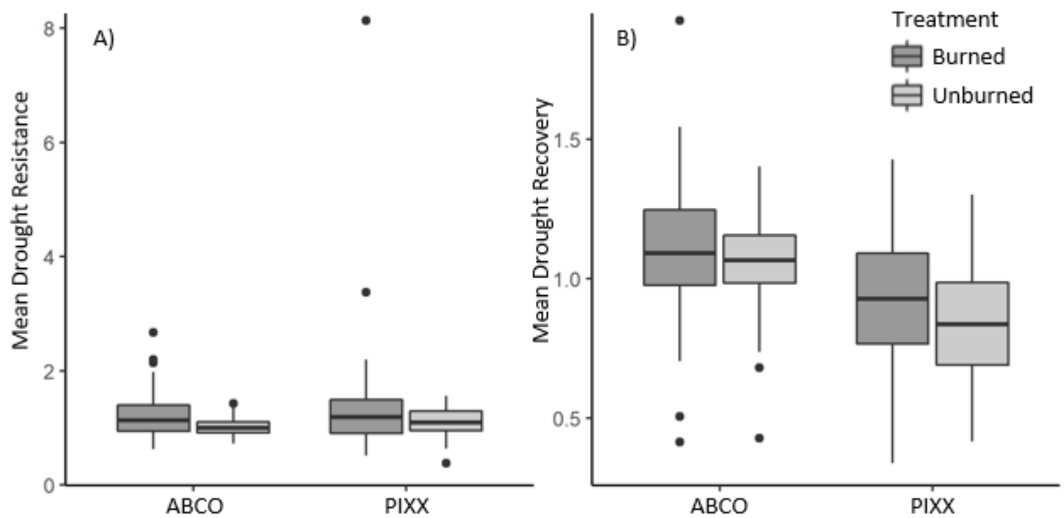

Figure 12. Mean drought resistance (A) and drought recovery (B) by species (ABCO = white fir; PIXX = yellow pine) for drought years (2007 – 2015) and subsequent recovery years (2016 and 2017), respectively, in burned and unburned treatment sites. Note the different y-axis scales between figures. Boxes represent coverage of the 25th and 75th percentiles, with whiskers showing the inter-quartile range.

DISCUSSION

Despite sampling a wide range of trees in a variety of competitive environments in both burned and unburned stands, results suggest forest management treatments reducing competition (thinning, prescribed fire, or both) should improve radial growth response of residual trees, including in times of below average moisture availability. For example, trees experiencing lower competition, regardless of treatment history, typically showed an increase in annual radial growth, as measured by BAI. Multiple factors contributed to the rate of BAI over the duration of the study period including crown ratio, competitive pressures, and yearly precipitation totals. Growth patterns varied between species, location, and history of prescribed fire treatments suggesting careful consideration of local forest structure when implementing forest management decisions aimed at improving likelihood of tree survival during impending drought.

Prescribed fire treatments were implemented well prior to the years analyzed for growth, allowing trees and their associated growing environments sufficient time to recover from any prescribed fire injuries. Following fire trees experiencing high crown scorch and bole char will display reduced BAI, although growth may increase due to fire-caused nutrient mineralization (Busse et al. 2000; Certini 2005; Feller and Klenner 2011; Renninger et al. 2013). These effects are generally transient (1 to 4 years post fire) and not expected to influence longer-term growth of the trees sampled. Additionally, only living trees were sampled in 2018, potentially excluding drought-sensitive individuals that may already have succumbed to drought-related mortality. This may bias findings

towards trees in environments suitable for survival during the postfire interval, while excluding trees that may have suffered the most extreme drought related effects (mortality).

Influences on Growth Patterns

Crown ratio can be used as a proxy for individual tree vigor (Hasenauer and Monserud 1996) and proved to be an important variable for predicting annual radial growth within this study. As crown ratios increase, one may expect to see increased photosynthetic potential and leaf surface area, and thus improved radial growth even during periods of low precipitation. Both species sampled within burned stands had slightly higher crown ratios compared to trees sampled within unburned stands. This supports other studies showing thinning activities may have the ability to increase tree crown ratios (Gillespie et al. 1994) and improve radial growth rates.

Trees within lower competitive environments grew at a significantly higher rate compared to trees experiencing highly competitive surroundings, supporting a number of previous studies (Biging and Dobbertin 1992, Das 2012, Vernon et al. 2017). Furthermore, findings suggest that as competition increases the benefits of a high crown ratio are diminished and appear to cease a relationship with growth. This could be due to the costs of maintaining high crown ratios that have considerably greater water demands and may act as a liability when competition is high and resources, such as water and nutrients, are limited. These findings suggest thinning treatments may be effective in creating an improved growing environment for residual trees, particularly during drought.

Comparing crown ratio of trees within burned and unburned sites appears to show a slight improvement of radial growth rates for trees within burned sites suggesting an additional unaccounted-for long-term benefit of prescribed fire.

Species-specific differences in response to treatment were found. In general, average DBH of white fir was lower than yellow pine, although white fir in both burned and unburned sites had higher annual growth rates compared to yellow pine. The differences in growth observed between species and tree size may largely be attributed to differences in shade tolerance, morphological traits (such as leaf area), and life history strategies that may lead to white fir success within highly competitive environments. Additionally, tree age may play a significant role influencing size-growth relationships; however, quality age data was not obtained. Both white fir and yellow pine responded positively to reductions in competition, although yellow pine showed only slight improvements in growth following treatment. White fir on the other hand, showed a significant improvement of growth in response to treatment.

Difference in radial growth measured between treatments was detected and suggests some influence of an unaccounted long-term effect of treatment. Unaccounted variability between treatments may stem from the omission of small diameter trees (<5cm DBH) that were not captured by the HI metric. Between treatment locations, small diameter trees (as well as shrubs), particularly at Butte Lake where a secondary treatment was carried out in 2004, were likely consumed by prescribed fire. The additional competition imparted by unconsumed trees may partially account for the variability detected among treatments.

Drought Resistance and Recovery

Study results suggest prescribed fire treatments targeting fuel reduction may not have significant effects on drought resistance or recovery in the mixed-conifer forests of LAVO during similar drought conditions. Trees within burned sites had slightly higher drought resistance and recovery, although competition did not seem to significantly influence drought resistance and was positively correlated to drought recovery. These findings contrast a number of studies showing a negative relationship between competition and drought resistance and/or recovery (Bottero et al. 2017) and the ability of thinning treatments to improve either of these metrics (Erickson and Waring 2014; Thomas and Waring 2015; Vernon et al. 2018). However, recent findings also show that prescribed fire may not always improve drought response (Callahan 2019), and competition may be less influential on radial growth during periods of climatic stress (Kunstler et al. 2011; Carnwath and Nelson 2016).

Neither species showed a significant difference in drought resistance or recovery related to treatment, although white fir exhibited slightly lower drought resistance and higher drought recovery compared to yellow pine. Species-level differences in drought resistance and recovery may be attributed to contrasting strategies to with drought related stress and water loss.

It is important to note that growth generally maintained the pre-drought trajectory throughout the duration of drought even without a significant treatment-related response in radial growth. A lack of detectible change during the drought may suggest that the low

moisture period identified was not severe enough to impart any substantial changes (neither positive nor negative) in growth (i.e., water availability may not have been a limiting factor). The lack of a standardized and quantified definition of drought in ecological studies may hinder an understanding of results and effects of drought on radial tree growth (Schwarz 2020). A widely accepted definition of drought would benefit future studies when comparing drought resistance and recovery metrics and attempting to identify consistencies (or lack thereof) across studies. Within this study, alternative drought years, including the widely cited 2012-2015 California drought (defined as a state emergency by the governor), produced similar results supporting the notion that regardless of specific drought years, recent drought conditions have not been severe enough throughout this region to impart negative growth effects (see Appendix C).

Management Implications

Analysis of tree growth allowed for the assessment of forest management treatments to reduce competition and improve annual radial growth during drought in mixed-conifer forests of Lassen Volcanic National Park (LAVO). Findings suggest the implementation of prescribed fire management, with adequate intensity and frequency, may successfully reduce live stem density and stand basal area and, in some cases, may be effective in alleviating competitive pressures of residual trees. While these results showed little effects in terms of improved drought resistance and recovery influenced by competition, increased BAI and crown ratio is an indication that such treatments may allow remaining trees higher likelihood to survive future more severe disturbance.

It is important to note that some management techniques may not be effective across all landscapes and forest types, and depending on target species, may accelerate growth of less desired species. Within this study, similar conditions were generally favorable for yellow pine and white fir indicating management prescriptions should acknowledge both species will respond to treatments similarly. This implies management intended to promote improved survival of yellow pine should place higher emphasis on removal of white fir, and vice versa.

Trees sampled within LAVO did not experience widespread tree mortality as observed throughout much of the Sierra Nevada during the recent historic drought. In part, this may be due to less severe drought effects throughout much of this region. However, as local climate variability continues to increase, it is imperative to inform forest managers of potential ways to adapt forests to changing environmental conditions and improve the likelihood of tree survival. Understanding when and where to implement thinning techniques should be at the forefront of forest management considerations as forest conditions continue to change.

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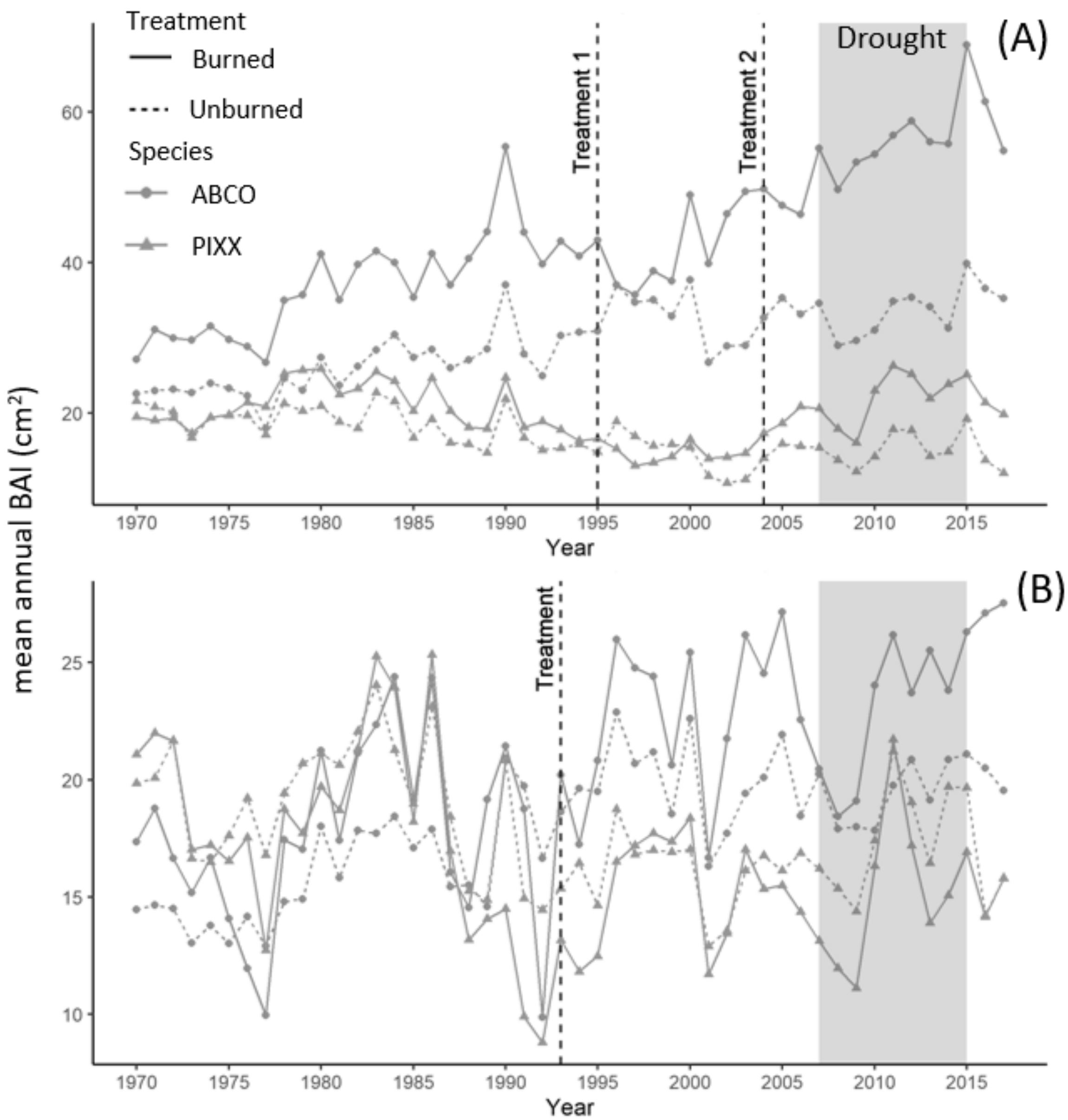
APPENDIX A

Appendix A: Mean drought resistance (DrResist) and recovery (DrRecov) (± 1 standard deviation) in burned and unburned locations grouped by location and species (ABCO = white fir, PIXX = yellow pine).

Location	**Species**	**Treatment**	**DrResist**	**DrRecov**
Butte Lake	ABCO	Burned	1.40 ± 0.47	1.03 ± 0.20
		Unburned	1.03 ± 0.15	1.08 ± 0.17
	PIXX	Burned	1.61 ± 1.20	0.90 ± 0.22
		Unburned	1.11 ± 0.24	0.82 ± 0.21
Knob Creek	ABCO	Burned	1.02 ± 0.19	1.19 ± 0.27
		Unburned	1.02 ± 0.15	1.03 ± 0.18
	PIXX	Burned	0.99 ± 0.37	0.98 ± 0.29
		Unburned	1.09 ± 0.23	0.87 ± 0.20

APPENDIX B

Appendix B: Time series (1970-2017) showing mean annual basal area increment (BAI) for yellow pine (PIXX; triangle) and white fir (ABCO; circle) trees in burned (solid line) and unburned (dashed line) sample locations within Butte Lake (A) and Knob Creek (B) site locations. The gray shaded area represents the period of recent drought (2007 – 2015). Note the different scale of y-axis between the two figures.



APPENDIX C

Appendix C: Model parameter estimates and variation for the top generalized linear mixed-effect models for drought resistance (DrResist) and recovery (DrRecov) when using Governor Brown's official declaration of emergency (2012 – 2016) as drought years. This analysis uses 2007-2011 as 'pre-drought' and a single year of recovery (2017). Model parameters include species, treatment, Hegyi competition index (HI), and crown ratio (CR). Parameter 95% confidence intervals (CI) estimated from 1000 bootstrap samples and standard error (SE) are shown.

Model	**Term**	**Estimate**	**SE**	**CI**
DrResist	Species (PIXX)	-0.01	0.03	-0.07 to 0.05
	Treatment (Unburned)	-0.04	0.03	-0.10 to 0.02
	HI	0.03	0.02	0.00 to 0.06
	CR	0.04	0.01	0.01 to 0.07
DrRecov	Species (PIXX)	-0.11	0.03	-0.16 to -0.06
	Treatment (Unburned)	-0.06	0.03	-0.12 to 0.00
	HI	0.03	0.01	0.00 to 0.06