RESTORATION AND TREE DROUGHT RESISTANCE IN COAST REDWOOD-DOUGLAS-FIR FORESTS AT REDWOOD NATIONAL PARK, CALIFORNIA

By

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ABSTRACT

DROUGHT & GROWTH RESPONSE OF COAST REDWOOD AND DOUGLAS-FIR IN RESTORATION SITES AT REDWOOD NATIONAL PARK, CALIFORNIA

Laura B. Lalemand

With the growing impacts of climate change worldwide and great uncertainty about forests' vulnerability to a changing climate in the Pacific Northwest, knowledge of coast redwood forest response is crucial. Many of the studies investigating forest response to drought focus on inland forest types rather than coastal forests. This study examined tree growth and drought response in coastal forests at restoration thinning sites, evaluating responses to local climate, tree-level competition, and site-level factors. Tree cores were extracted from previously harvested stands at three restoration sites in Redwood National Park, California, from both thinned and unthinned stands. Douglas-fir (*Pseudotsuga menziesii*) and coast redwood (*Sequoia sempervirens*) trees > 20 cm diameter at breast height were sampled (n = 274), spanning six different thinning prescriptions with varying years of thinning treatments (1978, 1995, and 2007). Generalized linear mixed effects models were used to evaluate the influence of local climate, competition, site, stand age, time since thinning, and species on tree growth and drought response. Competition was found to be negatively associated with tree growth for both tree species ($p < 0.0001$), and tree-level competition had a stronger influence on growth than climatic factors at all three sites. For both species combined, mean minimum

temperatures had a small negative effect ($p = 0.0073$) on growth, whereas mean annual precipitation had a positive effect on growth ($p < 0.0001$). The site closest to the coast and with the most recent thinning treatment harbored the fastest growing trees ($\mu = 2312$ mm^2 annually). Local competition had a strong negative effect on drought resistance during the recent drought (2012 to 2015) ($p < 0.0001$), and drought resistance did not appear to vary by treatment, site, or species. These results strongly suggest that restoration thinning treatments have the added potential of increasing tree growth and resistance to drought under current stand and climate conditions and possibly under future climate stress.

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INTRODUCTION

Rising temperatures, unprecedented precipitation patterns, and major disturbance events such as droughts are expected to increase and to continue to impact forests world-wide (Field et al. 2014). Widespread tree mortality and large stand die-offs have been documented in many forest types and tree species of western North America (van Mantgem et al. 2009; Allen et al. 2010). Research has attributed these events to increasing water deficits and drought in recent decades (van Mantgem and Stephenson 2007; Millar et al. 2012; Das et al. 2013; Williams et al. 2013). Rising temperatures and altered moisture patterns are driving additional stressors in North American forests such as pest and pathogen outbreaks and disturbance interactions (Weed et al. 2013). Disconcertingly, a recent review of existing research strongly suggests that we are underestimating forest drought vulnerability globally, especially in wetter forest types (Allen et al. 2015).

The findings of studies into forest resilience to drought vary across different regions and forest types. In the case of restored forests, research has demonstrated that the timing, intensity, and method of restoration thinning, as well as site conditions, can have substantial influence on drought response (Clark et al. 2016, Sanchez-Salguero et al. 2018). For example, Thomas and Waring (2014) found that thinned second-growth *Pinus ponderosa* stands exhibited increased resiliency and favorable stand conditions, such as larger tree sizes, greater radial growth, and greater resistance to and recovery from drought compared with unthinned stands. This research also found a strong relationship

between decreased radial growth and moderate to extreme drought conditions. In another study, Four years after thinning treatments, red pine (*Pinus resinosa*) resistance and resilience to drought was greater in heavily thinned sites compared with sites of less intensive thinning (D'Amato et al. 2013). Yet during a subsequent drought event, and after additional thinning treatments, the higher density stands receiving less intensive thinning treatments showed greater tolerance to drought than the more heavily thinned stands. This response reversal could be attributed to a number of factors including age or size-dependent threshold mechanisms, such as greater water demands in older or larger trees, thus leading to lower drought tolerance in this drier forest type.

Drought stress, along with other abiotic and biotic stressors, may have cumulative effects on tree growth and drought resilience. Research conducted on *Pinus edulis* die-back in the southwestern U.S. demonstrates that severe drought events could impose cumulative effects on surviving trees (Macalady and Bugmann 2014). Additionally, tree growth may exhibit resiliency thresholds related to cumulative effects rather than linear reductions in resiliency over time or with drought intensity. A study that is widely cited for the methodological approach (Lloret et al. 2011) found that resistance to drought events was positively correlated with past low growth events, but that drought resiliency was not correlated to past events. Their research suggests that understanding tree growth resilience and resistance components, as well as cumulative impacts, may be essential to understanding tree mortality and growth responses to stressors, such as severe drought. However, collectively thus far studies lack exploration of tree response to drought across varying tree-level competitive environments and for comparison of multiple tree species.

Across the western United States, drought conditions are expected to increase rapidly over the next century (Cook et al. 2015). On the north coast of California, research shows that between 1900 and 2000 average annual air temperatures increased by 1.6 ºC (Golightly et al. 2011) and the presence of summer fog decreased ~33% (Johnstone and Dawson 2010). Continued declines in summer fog frequency are predicted on the redwood coast (Johnstone and Dawson 2010). Recently, this region experienced a prolonged drought from 2012 to 2015, spanning moderate to exceptional drought conditions (United States Drought Monitor 2018). In California, climate models predict an additional 2 to 3.5 ºC rise in average annual temperature along with more frequent and large precipitation events (Cayan et al. 2008). With this rise in temperatures across California, forest-climate predictions suggest long-term shifts in species composition from needle-leaved trees to broad-leaved trees (Lenihan et al. 2003). Although old-growth coast redwood (*Sequoia sempervirens*) trees are unique in their long lifespans and infrequent mortality, some propose that the ranges of key tree species, such as coast redwood, could shift and even contract in response to climate change if tree mortality rates increase (Golightly et al. 2011; Fernandez et al. 2015).

Restoration treatments, such as mechanical thinning and prescribed fire, are used by managers in part to promote more vigorous tree growth and to increase forest resilience to disturbance. Past studies have shown that increased individual tree growth is associated with greater tree vigor and a lower probability of mortality (van Mantgem et al. 2003; Cailleret et al. 2017), and forest treatments that reduce stand density and forest fuels, resulted in less competition and canopy fuel hazards in interior second-growth

forests (Agee and Skinner 2005; D'Amato et al. 2013; Thomas and Waring 2014). Substantial tree growth responses have been observed in coast redwood-Douglas-fir forests in northern California following mechanical thinning treatments (O'Hara et al. 2010; Teraoka and Keyes 2011; Plummer et al. 2012).

Yet, it is unclear how redwood forests will response to future climatic conditions. Research on coast redwood growth in response to climate found varied responses in old-growth trees to climate across the redwood range (Carroll et al. 2014), and there is much uncertainty as to how coastal forests will respond to continued climate stress and potential cumulative impacts. Moreover, much of the redwood landscape today is severely altered. Until recently, old-growth coast redwood forests covered approximately 700,000 ha over their range. Today less than 5% of that old-growth redwood forest remains due to commercial clearcutting over the past century. In many cases, historical timber management practices employed in the redwood region have resulted in homogenous coast redwood-Douglas-fir stands with even-aged structure and closed canopies, low understory vegetation development and diversity, unnaturally high stand densities, and poor quality habitat for many wildlife species (Veirs 1986; Teraoka 2012; van Mantgem and Das 2014). As a result, these young redwood forests may respond differently and possibly be more vulnerable than old-growth forests to the many stressors brought on by climate change.

The uncertainties surrounding climate change impacts on coastal forests pose complex management challenges and add to the many concerns surrounding the future of old-growth and previously harvested coast redwood-Douglas-fir ecosystems. As climate

patterns shift, there is a need for greater understanding of whether current management practices are promoting resilient forests that can withstand and/or recover from increased climate stress such as drought. Yet, investigations of local competition, climate, and site conditions on tree growth response in previously harvested coast redwood-Douglas-fir forests are lacking. This study of tree responses to local climate and severe drought under varied management and forest conditions adds to the body of knowledge of forest response and vulnerability to climate, and will inform future restoration, stewardship, and adaptive management planning.

Objectives and Research Questions

This research was designed to identify patterns of tree growth response to climate and resistance to drought in young coast redwood-Douglas-fir stands under forest restoration thinning treatments. Tree-growth responses were compared under different local competitive environments and climatic conditions. Tree resistance to drought was estimated by comparing average tree growth before and during the recent drought event (2012 – 2015) and compared under the different local competitive environments and climatic conditions. Specifically, this study addressed the following research questions:

1) What are the effects of local competition, climate, and time since harvest or approximate stand age on coast redwood and Douglas-fir (*Pseudotsuga menziesii*) growth?

H1.1: Tree growth rates are greatest in treated stands with less competition and especially at sites with lower water stress (climatic water deficit) and with less time since harvest.

2) How does tree drought resistance change across different competitive and climatic environments, and which factors are most important?

H2.1: Resistance to drought is greatest for trees with less local competition, in stands that have lower climatic water deficit, that are closer to the sea, and that have had restoration thinning.

METHODS

Study Sites

Coast redwood exist in a thin, 724 km strip along the Pacific Coast, spanning from the southern border of Oregon to Monterey County in central California (Sawyer 2007). This study focused on previously harvested coast redwood forests in the northern part of their range, located in Redwood National Park, Humboldt County, California. Standing biomass in these redwood forests can reach well over 3,000 tons/ha. The shrub and herbaceous layers vary from dense to open and are primarily made up of black huckleberry (*Vaccinium membranaceum*), salmonberry (*Rubus spectabilis*), salal (*Gaultheria shallon*), coast rhododendron (*Rhododendron macrophyllum*), and western sword fern (*Polystichum munitum*). Along with coast redwood, other common conifers in these forests include Douglas-fir, western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*), but hardwoods such as tanoak (*Notholithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) are also commonly found (Noss 1999). Coast redwood is a fire adapted species; evidence of fire in coast redwood forests is found in the numerous fire scars observed along boles of old redwood trees and from fire history studies (Brown and Swetnam 1994; Lorimer et al. 2009). Although fire appears to be an important element of coast redwood forest systems, during the past century fire has been mostly excluded from northern coastal redwood forests, and the long-term effects of fire exclusion on these stands and future disturbance patterns are unknown.

Redwood National Park falls within the coastal subregion of the Klamath Mountain region. This cool, temperate region has mean annual temperatures of approximately 15 ºC and mean annual precipitation is typically greater than 100 cm, falling mostly as winter rain (NWS: http://w2.weather.gov/climate/local_data). Although this subregion has a Mediterranean climate, the dry summers are typically moderated by coastal fog, stratus clouds, and cool temperatures creating a dynamic climate in this coastal region (Sawyer 2007).

Redwood National Park has more than 21,000 ha of second-growth or previously harvested redwood forests with poor forest conditions. In response to this, the park has developed a forestry program that employs active management by means of restoration thinning to improve forest conditions. The goals of restoration thinning in young coast redwood forests are to decrease stand density, shift species composition towards historically occurring compositions, promote growth of remaining trees and understory vegetation, develop multi-storied canopies, to connect fragmented old-growth, and ultimately to promote forest maturation towards old-growth forest conditions (National Park Service 2008; Teraoka and Keyes 2011).

Three study sites were selected, spanning a range of experimental restoration thinning treatments located in young coast redwood-Douglas-fir forests within Redwood National Park in northwestern California (Figure 1, Table 1). The young coast redwood-Douglas-fir sites sampled were previously clearcut, resulting in stands with relatively even-aged cohorts containing continuous canopies, high stem densities, and a high proportions of Douglas-fir in relation to coast redwood. For comparison, in old-growth

stands of Redwood National Park, densities of coast redwood range between 24 and 44% and Douglas-fir range between 5 and 26%, but species composition in many of the previously harvested forests display more Douglas-fir dominant stands with coast redwood ranging from 27% to 39% and Douglas-fir from 35 to 62% (van Mantgem and Das 2014). Other less common tree species present in the study sites included western hemlock, Sitka spruce, grand fir (*Abies grandis*), tanoak, Pacific madrone (*Arbutus menziesii*), and off-site Port-Orford-cedar (*Chamaecyparis lawsoniana*). At the time of restoration thinning (1978 to 2007) stands had different ages, but were in the stem exclusion phase of development.

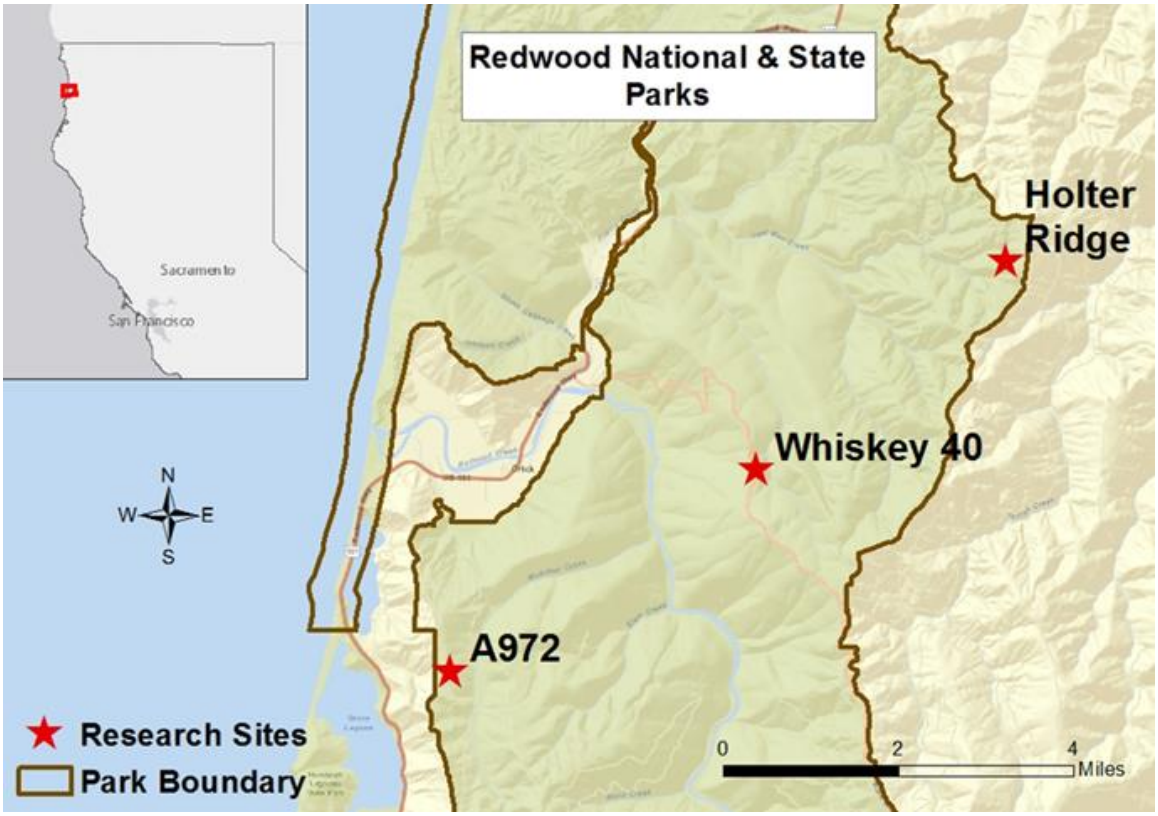

Figure 1. Site map showing treatment sites in second-growth redwood-Douglas-fir stands in Redwood National Park, and an inset regional map of northern California.

Table 1. Restoration and site information for research sites sampled in Redwood National Park.

Site	Site Area (ha)	Sampled Area (ha)	Stand Age in 2015	Stand Age at Time of Thinning	Thin Date	Distance To Sea (km)	Elevation (m)
A972	18	1.6	47	39	2007	2.4	304
Whiskey 40	16	0.74	52	32	1995	7.3	481
Holter Ridge	80	1	61	24	1978	11.3	462

Study Design

Within the study sites, previously established research plots containing six treated (thinned) and three untreated (control) areas were sampled for a total of nine plots (Table 2). Research plots were chosen to span the range of restoration thinning treatment types, thinning intensities, and stand ages at time of thinning that existed in the park (Chittick and Keyes, 2007; Teraoka and Keyes, 2011). Plots ranged in size from 0.06 to 0.25 ha. Topography varied across the study sites where values at the A972 site ranged from approximately 0 to 35 % slope and 45 to 225° aspect, at the Whiskey 40 site all plots had slopes of 15% and aspects of 90°, and at the Holter Ridge site slopes ranged from 15 to 40% and aspects from 270 to 315°. In each plot, all coast redwood and Douglas-fir trees ≥ 20 cm diameter at breast height (DBH; 1.37 m from the base of the tree) were sampled. All sites were clearcut in 1954 to 1968 and were subsequently thinned between 1978 and 2007 (Figure 2). Thinning methods included crown thinning (removal of trees in dominant and co-dominant crown classes) and thinning from below (removal of trees from lower

crown classes). Thinning prescriptions included single-entry treatments with varied reductions in basal area (20% to 55%).

Table 2. Number of sampled trees per each restoration thinning treatment group in Redwood National Park. SESE = *Sequoia sempervirens* and PSME = *Pseudotsuga menziesii*.

Site	**Treatment Group**	**Thinning Prescriptions**	**Thinning Method**	**SESE sampled**	**PSME sampled**	**Total sampled**
A972	L20	20% reduction in BA	Low	9	12	21
	L55	55% reduction in BA	Low	4	10	14
	H20	20% reduction in BA	Crown	11	8	19
	H55	55% reduction in BA	Crown	4	9	13
	ConA972	Control	NA	9	12	21
Whiskey 40	ThinA	30% reduction in BA	Low	23	27	50
	ConA	Control	NA	10	17	27
Holter Ridge	ThinHR	20-25% reduction in BA	Low	24	22	46
	ConHR	Control	NA	32	31	63
			Totals:	**126**	**148**	**274**

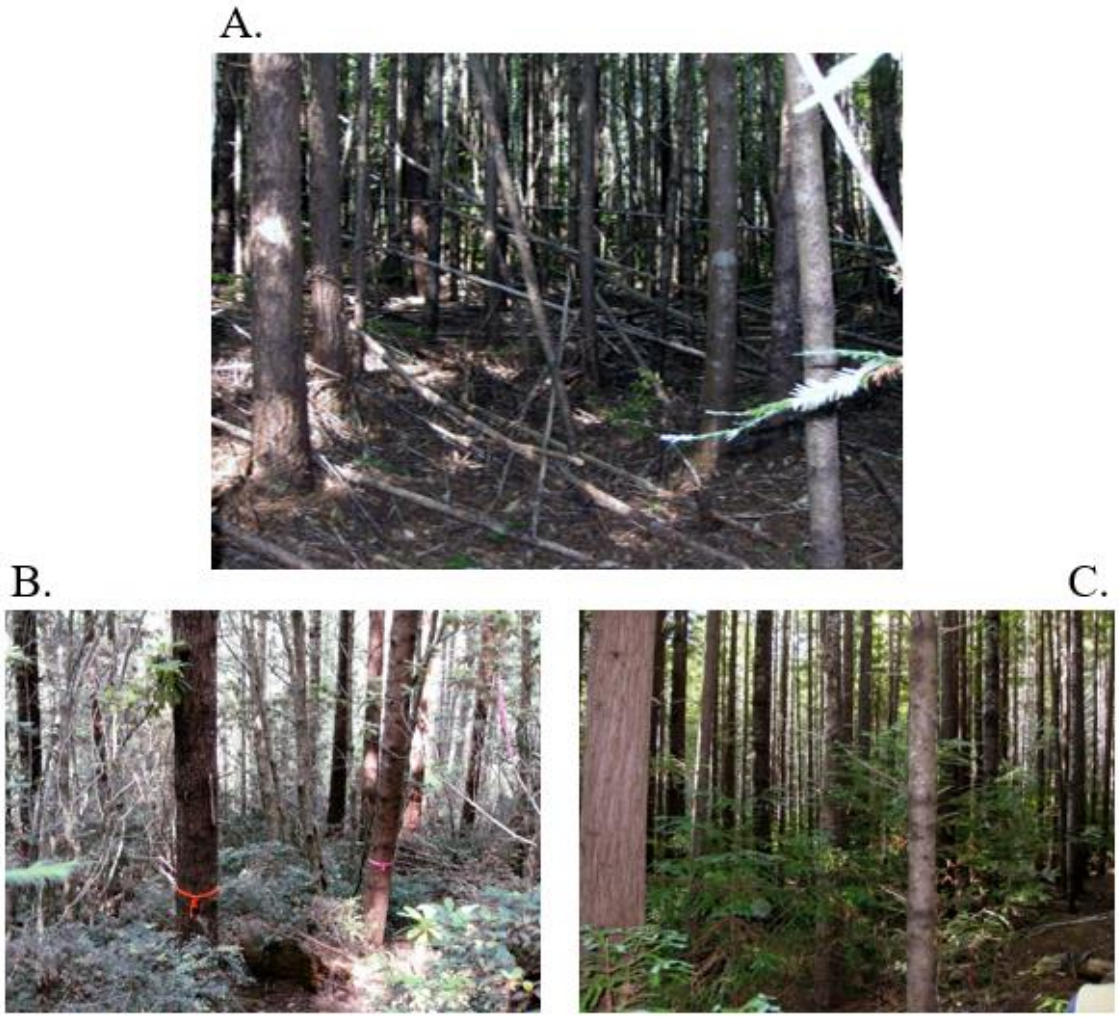

Figure 2. Example of forest conditions at the study sites, including an unthinned or control plot (A), a plot that received restoration thinning in 1978 (B), and a plot that was thinned in 1995 (C).

Field Methods

Sampling occurred in the summer of 2014 through the winter of 2015. At each tree a unique ID, status (dead or alive), and DBH measurement were recorded. Bark thickness was measured in the laboratory using digital calipers and a dissecting microscope for a subset of trees (n = 257). Any tree damage or unusual conditions were

noted. Tree cores were extracted from all trees ≥ 20 cm DBH at approximately 1 m above the base with a 4.3 mm increment borer. A single core was extracted from all trees < 40 cm DBH, while two cores were taken for all trees > 40 cm DBH. All second cores were taken at an angle perpendicular (i.e., 90 º) to the first core. When one or more cores were of poor quality (rot, unreadable rings, or missing pieces), this was noted, and the best quality core was given priority in core processing and analysis. Duplicate cores were also taken for smaller trees (< 40 cm DBH) if the initial core collected was of poor quality. Cores from dead trees and trees with notable physical damage (e.g., bear damage) were excluded from analyses (n = 40).

Laboratory Methods

Tree cores were affixed to wooden mounts and sanded using gradually finer sandpaper from coarse 100 grit to fine 600 grit. Mounted cores were scanned at 1200 resolution dpi or greater, and WinDENDRO (Regent Instruments 2014) was used to measure annual radial tree growth for each core to an accuracy of 0.001 mm. When two or more cores were collected, the annual growth measurements for each year were averaged. If one or more of the cores from the same tree were of very poor quality (rot, unreadable rings, and missing pieces, n = 100), they were excluded from analysis and only the higher quality cores were used for this study.

Tree cores were visually cross-dated by species and treatment group by counting rings and identifying marker years. Although attempted, the software program COFECHA could not be used to verify crossdating with correlation analysis because tree

core records were not long enough (Holmes 1983). Only visually cross-dated cores were used for tree growth, climate, and drought response analysis (n = 274).

Competition Metrics

Local competition for each tree was estimated by constructing a unitless, distance-dependent Hegyi competition index (Hegyi 1974). Competition index values were calculated using the equation:

$$(1) \qquad \text{competition}_i = \sum_{j \neq i} \frac{DBH_j}{DBH_i \times (Dist_{ij}+1)}$$

where DBH_i is the DBH of the subject tree (cm), DBH_j is the DBH of the neighbor tree DBH (cm), and $Dist_{ij}$ is the distance (m) between the subject tree and neighbor tree. Competition from all neighboring trees within 10 m of each subject tree (van Mantgem and Das 2014) was summed to calculate distance-dependent local competition values for each tree (

Table 3).

Table 3. Predictor means and standard deviations (unstandardized) by study site.

Term	A972	Whiskey 40	Holter Ridge	All Sites
BAI (cm^2)	23.1 ± 18.1	12.5 ± 8.1	22.8 ± 20.5	20.3 ± 18.5
BAI pre-drought (cm^2)	21.3 ± 15.8	12.9 ± 7.9	23.1 ± 20.7	20.6 ± 18.6
BAI during-drought (cm^2)	24.9 ± 20.0	10.9 ± 8.7	19.3 ± 18.8	18.8 ± 17.9
Drought Resistance Ratio (DrResis)	1.17 ± 0.41	0.96 ± 0.30	1.04 ± 0.48	1.06 ± 0.42
Competition Index (CI)	2.88 ± 1.46	3.62 ± 1.11	3.28 ± 1.68	3.32 ± 1.55
Tree DBH (cm)	33.0 ± 8.6	31.1 ± 8.2	42.5 ± 17.4	36.3 ± 13.8
Tree Basal Area (BA, m^2)	0.091 ± .050	0.081 ± 0.047	0.166 ± 0.157	0.118 ± 0.11
Time Since Treatment (yrs)	1 - 8	1 – 20	1 - 37	1 - 37
Time Since Harvest (yrs)	39 - 47	32 - 52	24 - 61	24 - 61
Annual Precipitation (cm)	158.7 ± 45.9	228.6 ± 55.4	234.9 ± 45.9	224.7 ± 60.8
Minimum Temperature (ºC)	6.8 ± 1.14	6.4 ± 0.8	6.45 ± 0.	6.49 ± 0.8
Maximum Temperature (ºC)	16.5 ± 0.9	17.7 ± 0.7	18.28 ± 0.62	17.95 ± 0.9
Climatic Water Deficit (mm)	220.3 ± 140.9	373.8 ± 102.1	209.0 ± 83.4	250.84 ± 119.21

Climate Data

Monthly regional climate data was obtained from the California Basin Characterization Model (BCM: http://climate.calcommons.org/bcm), a 270 m grid cell of climate and hydrology dataset provided by the Climate Commons (Flint et al. 2013; http://climate.calcommons.org/). Using R (R Core Team 2017), the data were summarized to estimate annual climate data for the calendar year at each study site. Climate variables used in the final analyses included annual climatic water deficit (CWD, in mm), annual precipitation (PPT, in mm), mean annual minimum temperature (TMN, in ºC), and mean annual maximum temperature (TMX, in ºC) (Figure 3, Table 3).

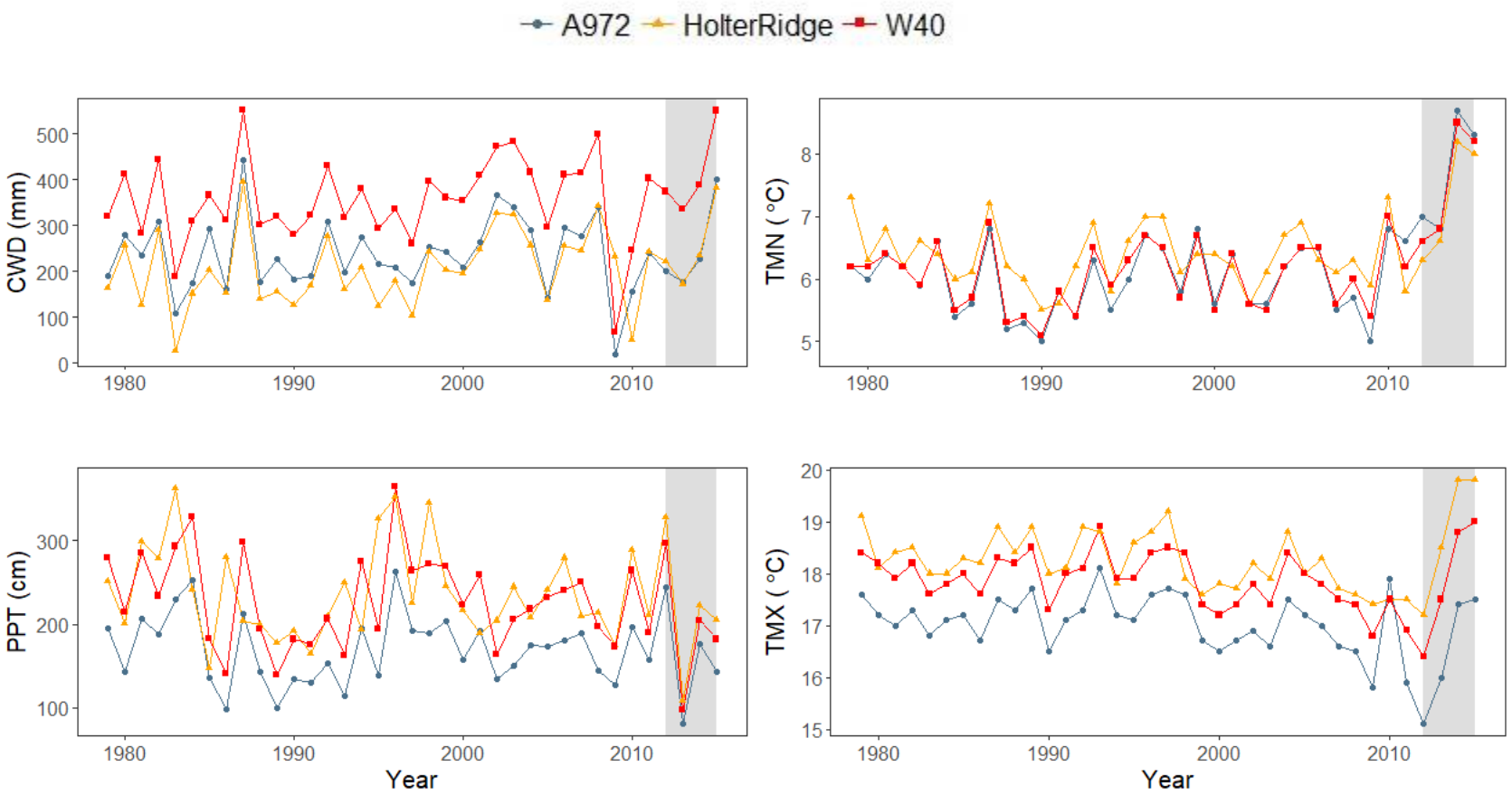

Figure 3. Estimated mean annual climatic water deficit (CWD), precipitation (PPT), minimum temperature (TMN), and maximum temperature (TMX) for the period of record (1979 - 2015) at the three study sites. Shaded area indicates the most recent drought period (2012-2015).

The period of recent drought (2012 to 2015) was determined using the United States Drought Monitor (USDM), which is the standard used for national drought conditions synthesis and reporting and is produced in collaboration by the National Oceanic and Atmospheric Administration, U.S. Department of Agriculture, and the National Drought Mitigation Center. The USDM characterized the California North Coast region as being in a moderate to extreme drought from 2012 to 2015 (USDM 2018). Once obtaining the general drought window for this region from USDM, the downscaled BCM climate data was then evaluated for each research site to see whether the USDM drought period was reflected in the local plot climate data. Two sample t-tests were used to test whether the mean drought-period climate values were significantly different from pre-drought values (1950 to 2011). T-tests showed that during the drought period, mean CWD ($p = 0.0447$), PPT ($p = 0.0248$), and TMN ($p < 0.0001$) were all significantly different from pre-drought conditions. TMX was not significantly different ($p = 0.7292$).

Tree Growth Response

Basal area increment (BAI) is an estimate of the area of wood produced by a tree during a given growing season. BAI was used as a measure of tree growth instead of raw ring width measurements to better represent annual wood production of a tree at different tree diameters. BAI (cm^2) was calculated for each year in each tree series using the dplR statistical package in R (Bunn 2008; Bunn et al. 2018). First, bark thickness (BT) was either measured in the laboratory or estimated using locally derived regression equations:

(2) $Douglas - fir\ BT = 3.035 + 0.420 * Diam$

(3) $coast\ redwood\ \ BT = 9.939 + 0.722 * Diam$

where Diam is the tree diameter outside the bark at the height where the tree core was extracted. Next, tree radius inside the bark was estimated by subtracting BT from each tree's radius in R. The dplR statistical package was then used to calculate BAI for each year of growth starting from the outer-most growth ring. For this, the width of all outer rings was first subtracted from the radius inside the bark for each annual growth ring. Then total tree stem area was calculated for the inner radii of each annual growth ring and this value was subtracted from the stem area for the outer radii of that same growth ring to get BAI for that year of growth (Figure 4).

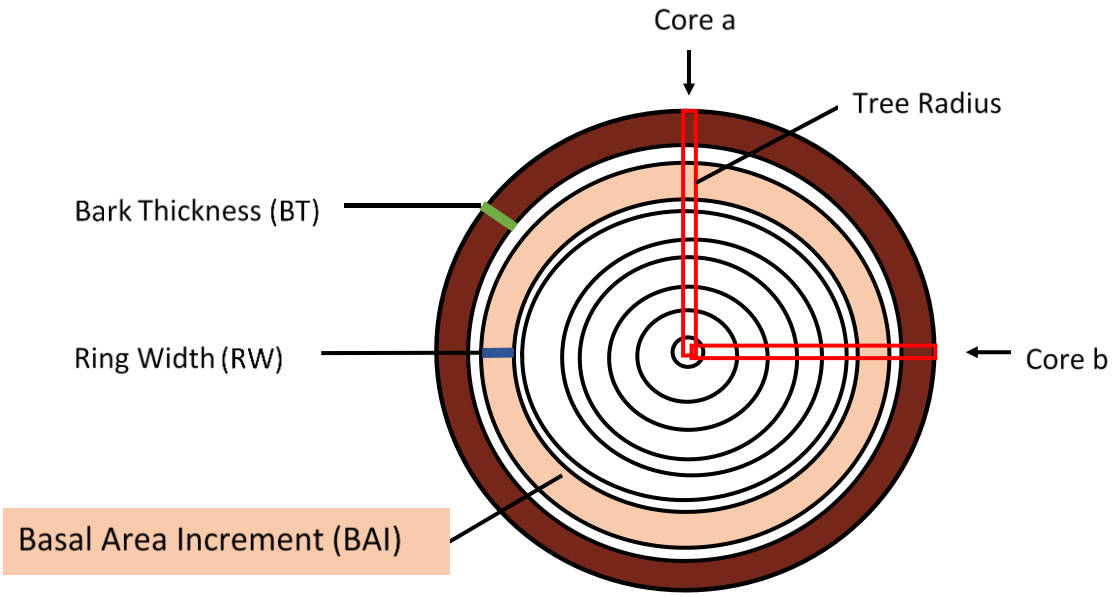

Figure 4. Diagram of a tree cross section demonstrating tree components, core extraction, and dendrochronolgy measurements and terms.

Tree Drought Response

Tree response to the most recent drought in this region from 2012 to 2015 was evaluated by estimating tree drought resistance (DrResis) for each tree using a ratio:

$$DrResis = {}^{DurDr}/_{PreDr} \quad (4)$$

where DurDr is the mean annual BAI for the 4 years during the drought and PreDr is the mean annual BAI for the 4 years preceding the drought (2008 to 2011) (Lloret et al. 2011). Therefore, DrResis values greater than 1 indicate increases in growth during the drought period (2012 to 2015) and drought resistance, values at 1 indicate no change in growth and therefore drought resistance, and values less than 1 indicate reductions in growth during the drought period or low drought resistance (Figure 5). The inverse equation of drought resistance or the ratio for tree drought response (PreDr/DurDr) was also analyzed, but this response variable was not used in final models.

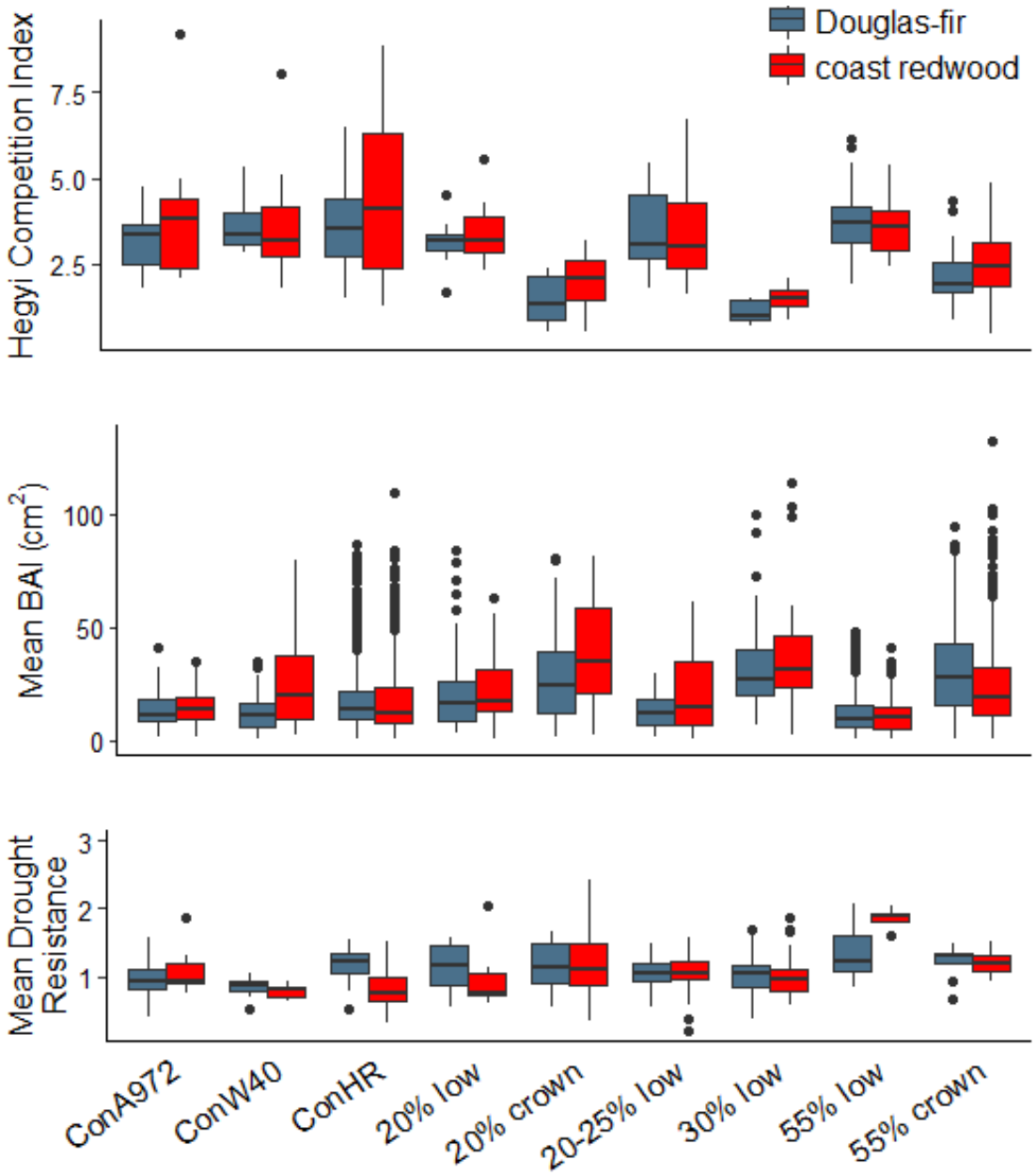

Figure 5. Hegyi competition index, mean basal area increment (BAI), and mean drought resistance for coast redwood (red) and Douglas-fir (grey) trees within all sampled treatment groups (x axis). ConA972, ConW40, and ConHR are trees from unthinned, control sites and all other treatment groups listed on the x axis had restoration thinning with the % basal area (BA) removed during thinning (20 to 55% reduction in stand BA) and the thinning method used (low or crown) identified in the title.

Statistical Analysis

To address both research questions, generalized linear mixed effects models (GLMM) were used with the lme4 package in R (R Core Team, 2017). The period of growth analyzed for Q1 included the first year post restoration thinning treatments at each site (Holter Ridge in 1979, Whiskey 40 in 1996, and A972 in 2008) through 2015. For Q2, growth data from 2011 to 2015 were analyzed (Figure 6). To address temporal autocorrelation in the Q1 time series model, the previous year's BAI was used as a predictor in all growth models. A gamma distribution was determined as the best fit to the model residuals for both analyses and a log-link function was chosen to relate the linear models to the response variables. To account for any spatial autocorrelation at the tree or treatment level, a random intercept on individual trees nested within treatment group was used for Q1 and a random intercept effect on treatment group was used to account for unmeasured treatment group variation for the Q2 models.

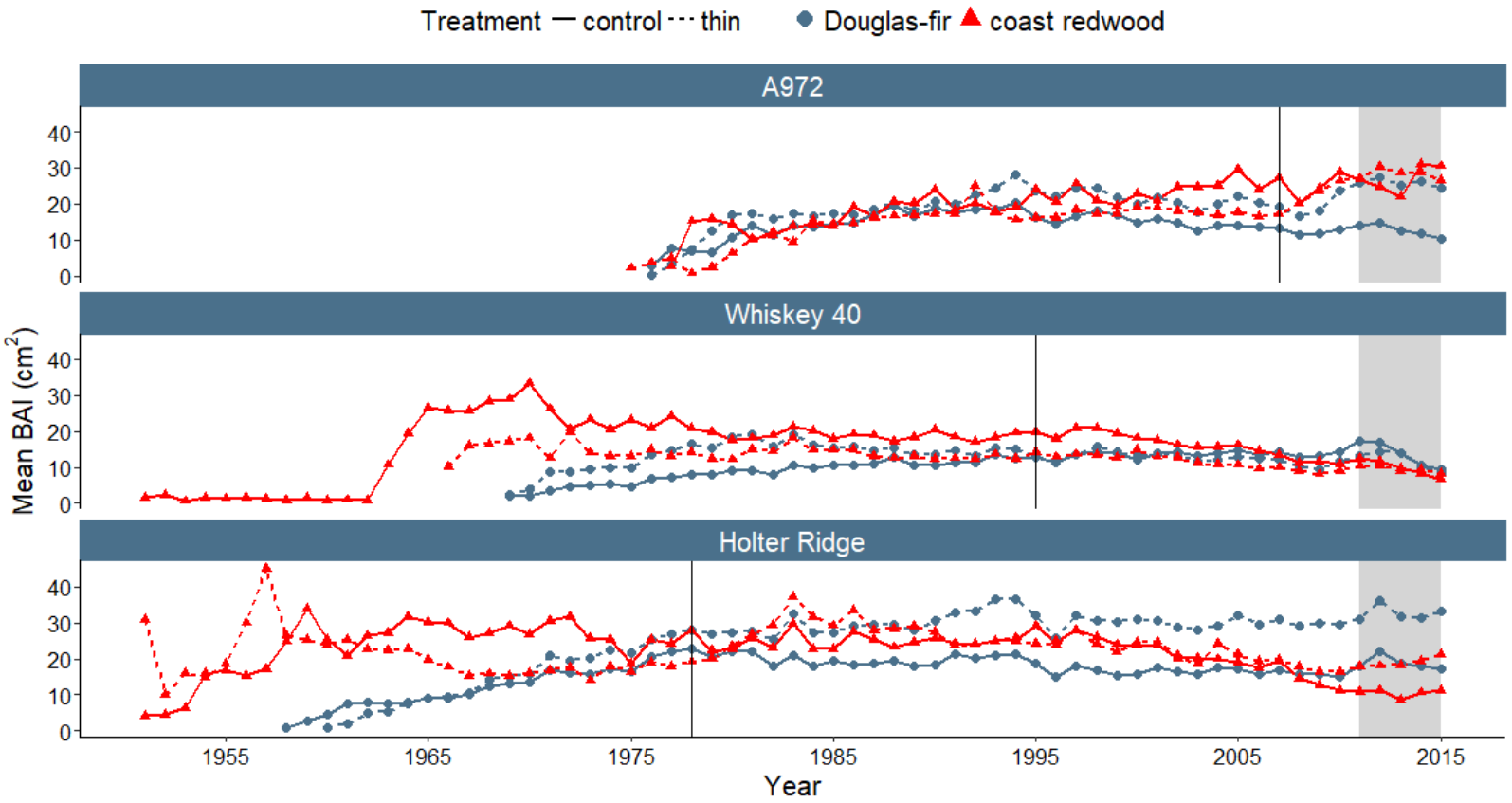

Figure 6. Mean basal area increment of coast redwood (dots) and Douglas-fir (triangles) from treated (dashed lines) and untreated (solid lines) stands at the three study sites. Shaded bar indicates the most recent drought period (2012-2015). Black vertical lines indicate the year of thinning treatment at each site.

Prior to any model design, all possible predictors were checked for multicollinearity using pairwise comparisons with Pearson correlation tests and an α of 0.05. Categorical predictors were visually assessed against continuous predictors using scatter plots and none were found to be confounded. All numeric predictors were then standardized using the center and scale method (value-mean)/standard deviation) for numeric stability due to the wide range of predictor scales. For each model, goodness of fit of the model to the data was determined by visually inspecting gamma quantile-quantile plots. Autocorrelation estimate plots were also used to check for autocorrelation in the model residuals and data were deemed acceptably uncorrelated when autocorrelation estimates were below 0.05. All models with acceptable goodness of fit and autocorrelation plots were then compared using Akaike Information Criteria (AIC) to identify models with the greatest explanatory power and variable parsimony (Zuur et al., 2009). Models within two AIC units were chosen as the top models and drop in deviance tests were then used to determine the importance of variables in the qualifying models for the final model selections. For all top models, 95% confidence intervals were used to determine variable importance and an α of 0.05 was used to determine variable significance.

RESULTS

Growth Response

Coast redwood and Douglas-fir growth is strongly related to local tree competition ($p < 0.0001$), mean annual precipitation ($p = 0.0002$), mean annual minimum temperature ($p = 0.0060$), and time since harvest ($p < 0.0001$). There was moderate evidence that growth response varied by species ($p = 0.0473$) (Figure 7). Trees with higher local competition had lower annual growth (BAI), and for every 1 SD increase in local competition (SD = 1.6) the model predicted a 28.4% reduction in annual growth (95% CIs: 24.3% to 32.2% reduction). Mean annual precipitation had a positive effect on annual growth, whereas mean minimum temperatures had a negative effect. For every 1 SD increase in mean annual precipitation (SD = 60.8 cm) the model predicted a 1.8% gain in annual growth (95% CIs: 0.8% to 2.8%), and for every 1 SD increase in mean minimum temperatures (SD = 0.8 °C) the model predicted a 1.1% reduction in annual growth (95% CIs: 0.4% to 2.2%) (Figure 8). With increasing time since harvest (years), the model predicted a negative trend on tree BAI where for every 1 SD increase in time since harvest or approximate stand age (SD = 9 years), BAI was expected to decrease by 10.9% (95% CIs: 10.0% to 11.7%) (Figure 9). Holding local competition, precipitation, minimum temperature, and time since harvest equal, coast redwood had 10.0% greater annual growth (95% CIs: 0.3% to 21.3%) than Douglas-fir.

The model results for tree growth from all trees in treated or thinned stands, that also included time since thinning treatment, showed similar effects. Time since treatment had a significant effect on BAI with the model predicting a 10.9% decrease in growth for every 10-year increase in time since restoration thinning (95% Cis: 10.8% to 11.1%) (Figure 10).

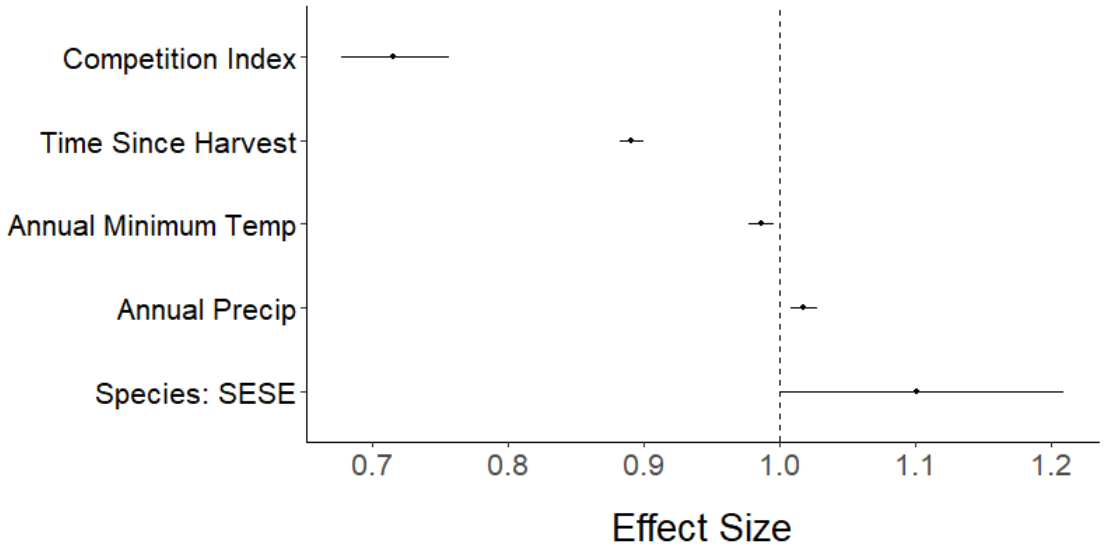

Figure 7. Multiplicative effect size of predictor variables on basal area increment (BAI) in the final generalized linear mixed effects model on *Sequoia sempervirens* and *Pseudotsuga menziesii* growth. Values have been backtransformed and represent multiplicative effects on BAI per 1 SD increase in predictor values where effects < 1 represent negative effects and values > 1 represent positive effects. Bars represent 95% confidence intervals. SESE = coast redwood.

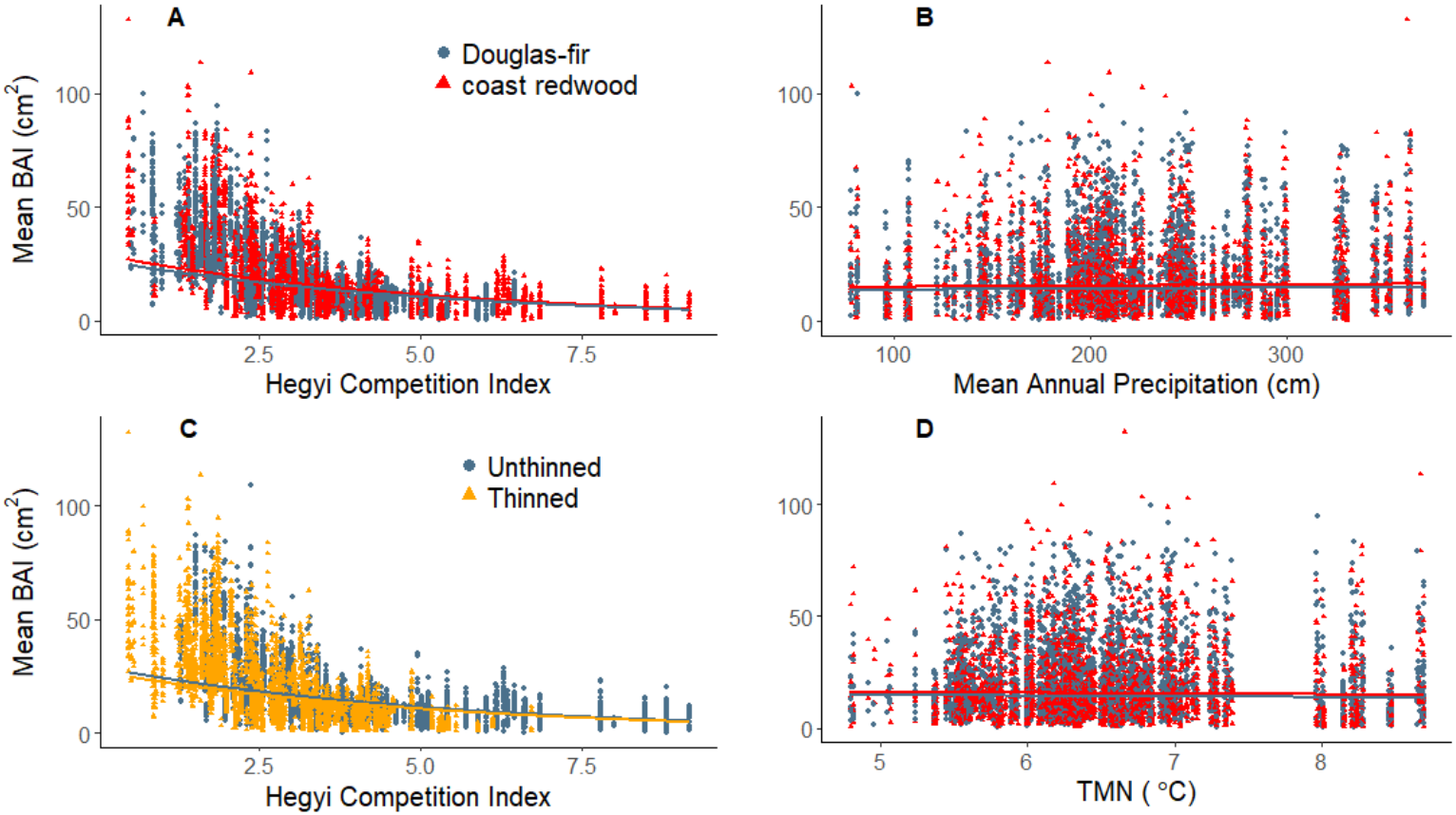

Figure 8. Scatterplots showing the relationships between basal area increment (BAI) and the Hegyi competition index (A and C), mean annual precipitation (B), and mean minimum temperature (D). Points represent the observed data of BAI per tree per year and lines represent model fitted values. Model results show the effect of each predictor variable on basal area increment (BAI) while holding all other predictors at their means and excluding random effects. Coast redwood is represented by red triangles and Douglas-fir by grey dots in plots A, B, and D. Unthinned (grey dots) values are from control stands and thinned (yellow triangles are from treated stands in plot C.

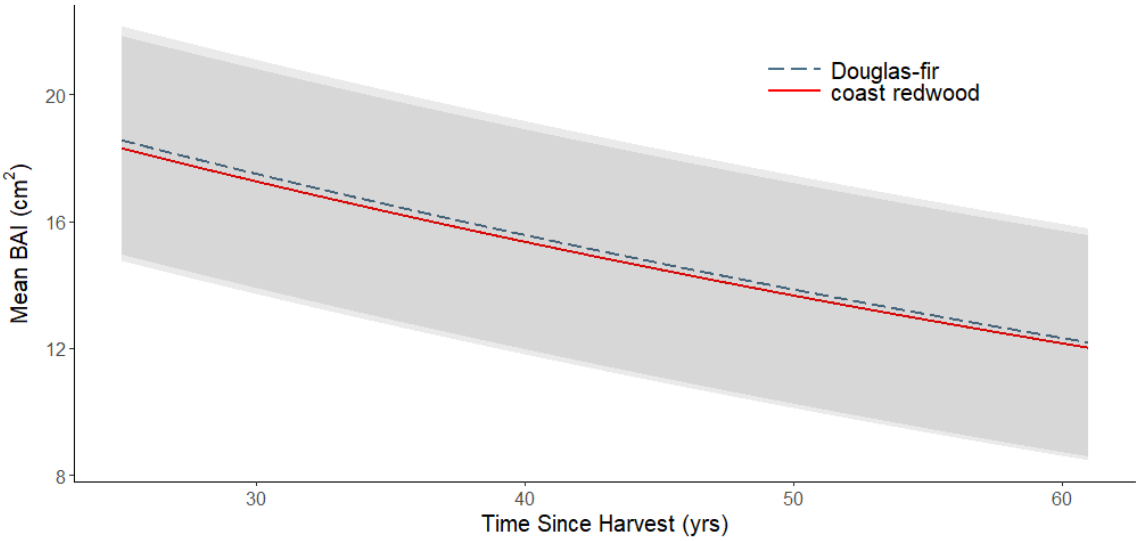

Figure 9. Prediction plot showing the relationships between basal area increment (BAI) and time since harvest. Lines represent model fitted values for coast redwood (red solid line) and Douglas-fir (grey dashed line). Model results show the effect of time since harvest on basal area increment (BAI) while holding all other predictors at their means and excluding random effects. Line shading indicates 95% confidence intervals.

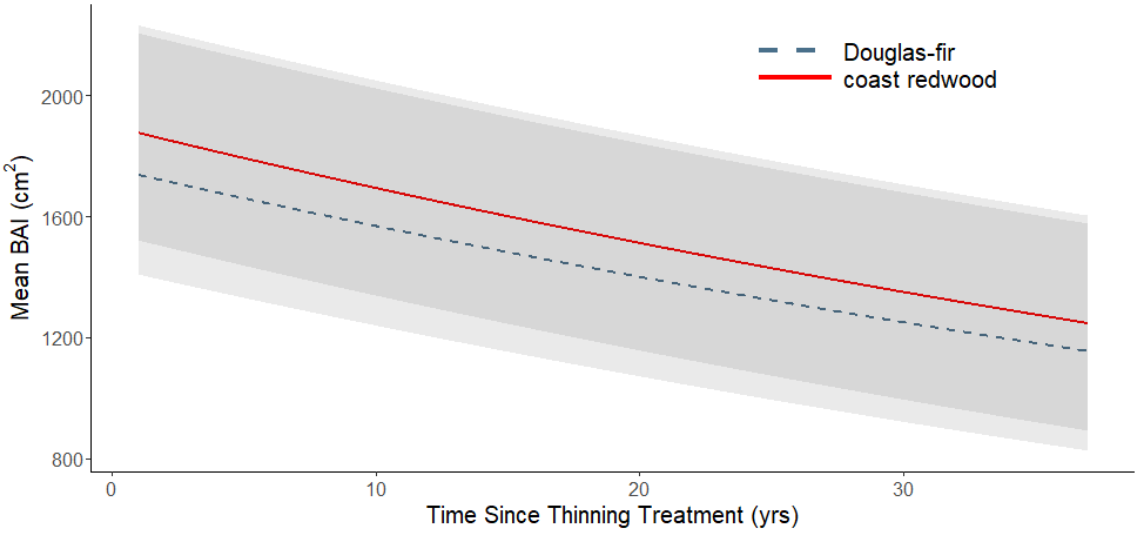

Figure 10. Prediction plot showing the relationships between basal area increment (BAI) and time since thinning treatment. Lines represent model fitted values for coast redwood (red solid line) and Douglas-fir (grey dashed line). Model results show the effect of time since treatment on basal area increment (BAI) while holding all other predictors at their means and excluding random effects. Line shading indicates 95% confidence intervals.

For tree growth response, the linear predictor for the best model took the form of:

(5) $$BAI = \beta_i - 0.716^{CI} + 1.018^{PPT} - 0.987^{TMN} - 0.891^{TSH} + e^{random\ effects}$$

When evaluating just treated stands with a model that replaces time since treatment with time since thinning treatments, the linear predictor took the form of:

(6) $$BAI = \beta_i - 0.746^{CI} + 1.021^{PPT} - 0.993^{TMN} - 0.891^{TST} + e^{random\ effects}$$

Where β is the model intercept, *i* is species (*Sequoia sempervirens* or *Pseudotsuga menziesii*), CI is the Hegyi competition index, PPT is mean annual precipitation, TMN is mean minimum temperature, TSH is time since the original timber harvest in years, TST is time since thinning treatment in years, and *e* is the subject residuals (Table 4).

Table 4. Generalized linear mixed effects models for tree basal area increment (BAI) including predictors for competition index (CI), mean annual precipitation (PPT), mean annual max temp (TMX), mean annual min temp (TMN), climatic water deficit (CWD), treatment (thin or control), and species *(Sequoia sempervirens* or *Pseudotsuga menziesii*). Shaded area indicates models within 2 AIC, bold-lettering indicates the final model selection.

Model Predictors	**df**	**AIC**	**ΔAIC**	**weight**
CI + PPT + TMN + TSH + Species	**10**	**95985.4**	**0.0**	**0.47**
CI + PPT + TMN + TSH + Treatment + Species	11	95986.6	1.1	0.26
CI + PPT + TMN + TSH	9	95987.4	1.9	0.18
CI + PPT + TMN + TSH + Treatment	10	95988.7	3.3	0.09
CI + PPT + TMN	9	96535.8	550.4	0.00
CI + PPT + TMN + Species	10	96537.4	552.0	0.00
CI + PPT + TMN + Treatment	8	96537.5	552.0	0.00
CI + PPT + TMN + Treatment + Species	9	96539.1	553.7	0.00
CI + PPT + TMX	8	96557.5	572.1	0.00
CI + PPT	7	96603.5	618.1	0.00
CI + CWD + TMN	7	96619.6	634.2	0.00
CI + TMN	8	96624.6	639.1	0.00
CI + CWD	7	96627.5	642.1	0.00
CI	6	96681.2	695.8	0.00

Drought Resistance

Drought resistance was strongly related to local tree competition ($p < 0.0001$) where greater local competition resulted in lower drought resistance (i.e., reductions in growth) for trees during the drought period (Figure 11). For each 1 SD increase in local competition (SD = 1.6), the model predicted an 8.9% decrease in tree drought resistance

(95% CIs: 8.7% to 9.1%) for all trees (Figure 12). There were no differences in the competition effect of different tree species (SESE, PSME, or other) on the drought resistance of the study trees. Drop in deviance test results confirmed that including species, treatment, treatment year, tree basal area, and distance from sea did not improve the model. The inverse of drought resistance, drought response, was also explored using gamma GLMMs with similar results.

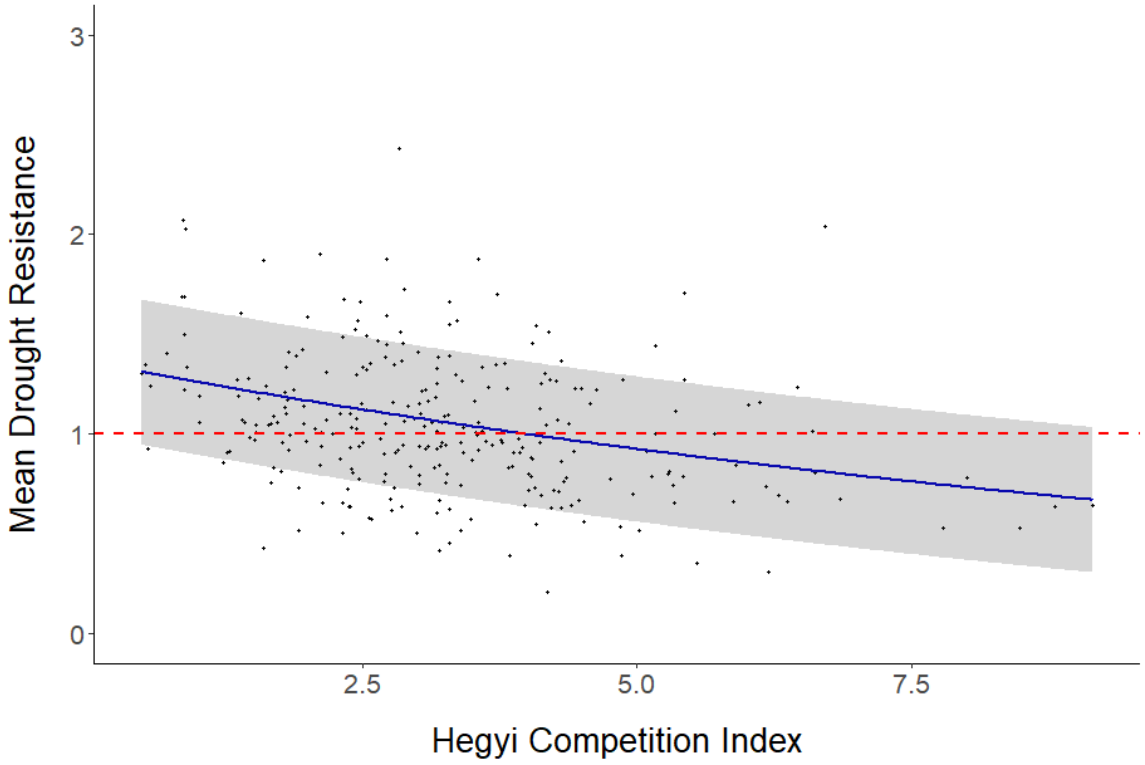

Figure 11. Scatterplot showing the relationship between mean drought resistance and the Hegyi competition index. Points represent the observed data, and the blue trend line with shading represents the model fitted values while excluding random effects. Line shading indicates 95% confidence intervals. Drought resistance values > 1 represent positive effects or increases in growth during drought, values < 1 represent decreases in growth during drought or low drought resistance, and values at 1 represent no change in growth during drought and thus drought resistance (red, dashed line).

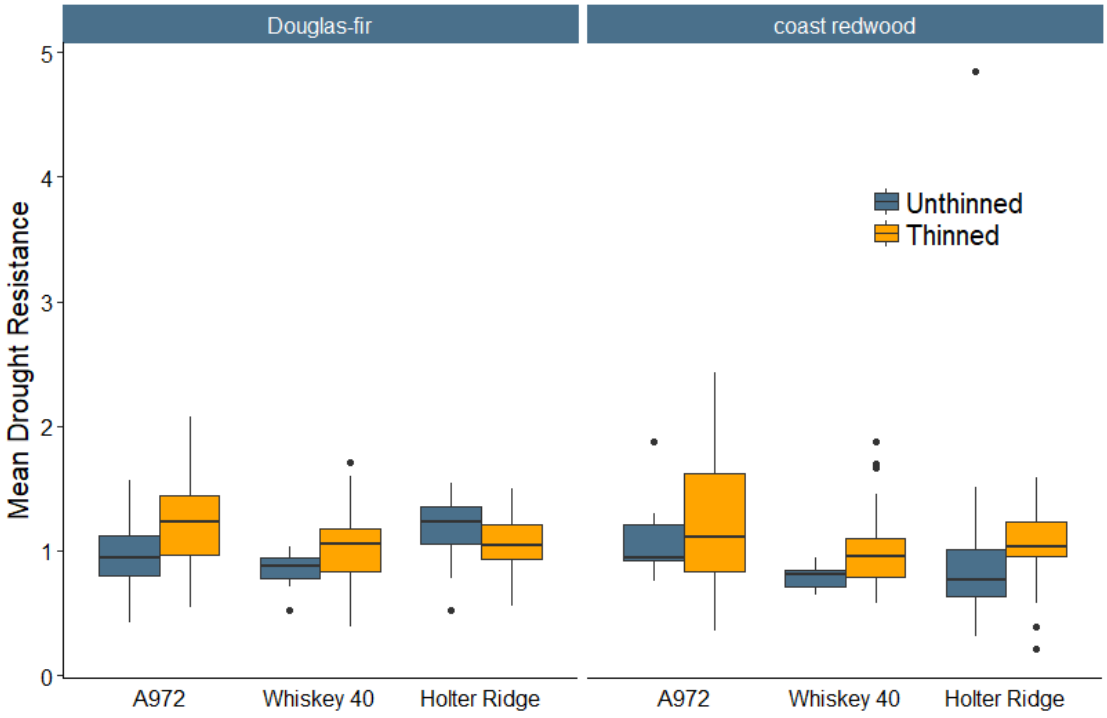

Figure 12. Mean tree drought resistance of coast redwood and Douglas-fir trees at unthinned (grey) and thinned (yellow) study sites.

For tree drought resistance, the linear predictor for the best model took the form of:

(6) $$Drought\ Resistance = \beta - 0.890^{CI} + e^{random\ effects}$$

Where β is the model intercept, CI is the Hegyi competition index, and *e* is the subject residuals (Table 5).

Table 5. Generalized linear mixed effects models for tree drought resistance including predictors for competition index (CI), relative competition index by tree basal area (relCI), tree basal area (BA), distance to the sea (DistSea), treatment (thin or control), treatment year (1978, 1995, or 2007), and species (*Sequoia sempervirens* or *Pseudotsuga menziesii*). Shaded area indicates models within 2 AIC, bold-lettering identifies the final model selection.

Model Predictors	**df**	**AIC**	**∆AIC**	**weight**
CI	**4**	**194.1**	**0.0**	**0.140**
CI *Species	6	194.3	0.2	0.124
CI + DistSea	5	194.6	0.4	0.112
CI + Treatment	5	194.9	0.8	0.096
CI + TreatmentYr	6	195.1	1.0	0.083
CI + BA	5	195.3	1.2	0.076
CI + Species	5	195.5	1.4	0.070
CI + DistSea + Treatment	6	195.8	1.7	0.060
CI + BA + Treatment	6	196.1	2.0	0.051
CI + Treatment + Species	6	196.2	2.1	0.049
CI + TreatmentYr + Treatment	7	196.5	2.4	0.042
CI * Treatment	6	196.6	2.5	0.040
CI + BA + Treatment + Species	7	197.8	3.7	0.022

DISCUSSION

Both hypotheses were partially supported by the study results: 1) tree growth rates were greatest in treated stands with less competition, and especially at sites with lower water stress (climatic water deficit) and with less time since harvest; and 2) resistance to drought was greatest for trees with less local competition, in stands that were thinned, that are closer to the sea, and at sites that have less climatic water deficit. I found that tree growth in the coast redwood-Douglas-fir forest restoration sites was strongly influenced by local tree competition and moderately influenced by regional climate factors over the study period (1979, 1996, or 2008 through 2015, depending on study site). Tree growth was also strongly influenced by the continuous variables of time since the original harvest (approximate stand age) and by time since thinning treatment, but not by a categorical treatment variable (thinned or control). Similarly, tree drought resistance was strongly influenced by competition for both tree species at all study sites. However, none of the other variables - distance to the sea, treatment, treatment year, CWD, and other climate factors - were strong influences on tree drought resistance.

Research has shown that changes in radial tree growth rates are indicative of changes in tree vigor and productivity (Dobbertin 2005). The observed trend of greater tree growth with decreasing tree competition in this study corroborates a growing body of literature on previously harvested coast redwood and Douglas-fir tree growth, suggesting that reduced competition via thinning significantly improves tree growth and vigor (Veirs 1986; O'Hara 1988, O'Hara et al. 2010). Recent work in coast redwood found that four

years after thinning treatments, trees with no crown competition had 33% greater annual basal area increment than trees surrounded by competitor trees (Dagley et al. 2018). Other research in young coast redwood-Douglas-fir forests found that tree-level competition explained up to 50% of the variation in growth across their study sites (van Mantgem and Das 2014).

My analysis adds to these studies and shows that individual tree growth decreases with greater water stress (decreasing PPT and increasing TMN), and with greater local competition. In the interior West, research found Douglas-fir trees experiencing high amounts of competition were more sensitive to abiotic stressors such as drought stress (Carnwath and Nelson 2016). However, I did not detect similar dynamics of climate and competition on annual tree growth at these coastal study sites. Nor did I find species or treatment (thinned vs. control) differences to be strong predictors of annual growth, as has been shown in treated red pine stands (D'Amato et al. 2013). The lack of a treatment effect coupled with the pronounced effect of local competition on growth could point to the greater importance of tree-level conditions rather than stand-level conditions or treatment type and intensity.

As hypothesized, as local tree competition increased, I found greater declines in growth at the onset of drought or lower drought resistance. Recent studies examining pine forests also found that reduced competition from forest thinning treatments had positive effects on tree resistance to drought (Lloret et al. 2011; Thomas and Waring 2014; D'Amato et al. 2013). However, I did not find stand categories such as treatment vs. control (untreated) to be influential to tree drought resistance, and rather tree-level

competition was much more important in my study. In addition, contrary to the findings of Lloret et al. (2011), I did not find subject tree size to be an important predictor of tree drought resistance. A key difference between studies was that the pine forests had not been logged (Lloret et al. 2011), as opposed to the even-aged second-growth stands of this study (with relatively lower variation in tree sizes). As variation in tree size expands with stand age and development, tree size may be important, and some research has revealed decreasing resilience and resistance to drought in trees with greater tree size (Bennett et al 2015; Merlin et al. 2015).

Across the three research sites, tree growth rates varied with the fastest tree growth observed at the A972 site. On average, trees at A972 accrued more wood each year over the period of record (2007 to 2015), especially during the drought period (2012 to 2015). Geographically, the A972 site is closer to the coastline and to sea level than the other two sites, however, estimated rainfall and mean maximum temperatures were lowest, and mean minimum temperatures were highest, at this site. Average local tree competition was also much lower at the A972 site than at the other two sites, supporting my findings of a stronger influence of local competition than climate on tree growth at this site. Additionally, year of timber harvest and of restoration thinning occurred more recently at the A972 site (1968 and 2007, respectively) than the other two sites, and is reflected in the lower levels of competition at the time of this study and during the recent drought period.

Site conditions appeared more favorable to coast redwood and Douglas-fir growth at the A972 site than the other two sites as reflected in the higher growth rates. It is

feasible that coastal fog conditions are more favorable than at the two more interior and uplands sites. Since local competition values were lowest on average at the A972 site that contributed to maximizing growth, resulting in the more vigorous or faster growing trees. If trees at the A972 site are in fact advantageously located (i.e., maximizing growth leading up to drought), this scenario supports the findings of Macalady and Bugmann (2014) on piñon pine, where trees that maximized their growth during wetter years had greater success during drier or drought years. If similar dynamics occur in second-growth coastal redwood forests following restoration thinning, they could illuminate meaningful spatial elements to consider when designing restoration treatments, within and across stands and fog gradients.

Coast redwoods had greater overall growth than Douglas-fir over the period of record, but coast redwood had greater relative declines in growth (or lower drought resistance) compared to Douglas-fir during the drought period, although species differences were not significant. Other studies have found varying species-level responses to water stress in coast redwood (Ambrose et al. 2015), other conifer species (Levesque et al. 2013), and in angiosperm tree species (Mitchell et al. 2012). Research suggests that during times of drought, several mechanisms result in decreased tree growth and greater tree mortality (Franklin et al. 1987; Allen et al. 2010; Allen et al. 2015), including reductions in carbon metabolism and increases in hydraulic failure. Research describes a hydraulic framework for tree mortality that suggests wetter years may actually heighten plant susceptibility to drought, and that this process can vary by species (McDowell et al. 2008). Interestingly, recent research found strong influences of site

conditions on tree drought response in cluster pine forests in the western Mediterranean Basin where trees in wetter sites show increased drought vulnerability compared with trees at drier study sites (Sanchez-Salguero et al. 2018). In the context of this study, perhaps greater water use efficiency by coast redwood trees contributes to faster radial growth, greater leaf area, reduced growth of roots and sapwood, and ultimately a higher relative hydraulic demand than that of Douglas-fir during wetter years in these young stands. Under this scenario, it is possible that species differences in drought resistance would become more pronounced with increasing drought stress.

I had expected that estimated water stress in the form of CWD would be the strongest climatic driver for predicting tree growth at these sites, but in fact I found that models including CWD did not fit the data best. Instead, mean annual precipitation and minimum annual temperatures were strongly associated with tree growth at all forest restoration sites and proved to be better climatic predictors of individual tree growth in the models. CWD estimates the evaporative demand in excess of the available soil moisture, and although both temperature and precipitation contribute to CWD estimations, they are only a portion of the inputs that are integrated into CWD calculations for estimating drought stress in a system. Research from other areas of the western U.S. (Restaino et al. 2016) suggests that Douglas-fir growth is more sensitive and correlated to integrated climate variables such as CWD than to the influences of precipitation and temperature alone. The stronger associations of precipitation and minimum temperature with coast redwood and Douglas-fir tree growth, rather than CWD, could be attributed to a number of factors.

First, these results could suggest that CWD is not an appropriate measure for drought stress in these maritime forest ecosystems. CWD incorporates location specific soil water storage into its estimates of drought stress, whereas other commonly used drought metrics assume uniform subsurface water storage (Alley 1984). Soil data for this area is coarse and I did not collect site specific soil data to feed into CWD calculations. Additionally, exploring other measures of drought stress that take into account water inputs from fog could have shown different trends. It is also a possibility that drought stress across the three coastally influenced sites (A972, Whiskey 40, Holter Ridge) was not severe enough or did not have enough variation to measurably influence tree growth significantly during the study period (1979, 1996, and 2007 to 2015). California's North Coast Drainage Climate Division (401) has been labeled in a moderate to exceptional drought from 2012 to 2015 (United States Drought Monitor 2018), but due to the importance of fog inputs in the redwood coastal region, measuring drought in this system is complicated. All three of these sites are marine influenced, located 2 to 12 km from the Pacific Ocean, and typically receive cool fog during the summer months. Summer fog is an important water source for coastal forests, with some studies estimating that fog contributes 25 to 50% of the water input to these environments (Dawson 1996, 1998). In addition, coast redwood is capable of absorbing fog through both foliage (Burgess and Dawson 2004; Burgess 2006) and bark (Earles et al. 2016), which may help to facilitate hydraulic recovery during times of water stress and/or low rainfall, particularly in the southern part of the species range.

Some recent studies have shown a significant decrease in summer fog or coastal low cloudiness on the Pacific north coast over the past 60 years (Johnstone and Dawson 2010; Schwartz et al. 2014), and reduced fog may be advantageous to tree growth in north coast forests. Reduced fog increases light availability in light-limited forests, and it has been estimated that 49% of coast redwood trunk wood volume increment is related to light availability (Coonen 2015). Across their range, growth rates of old-growth redwood trees exhibited significant increases in annual growth rates over the last century (Carroll et al. 2014 and Sillett et al. 2015). Measuring differences in fog and light availability could offer additional insight into the trends we see in growth and drought resistance, and could uncover additional dynamics in growth-climate relationships and drought response in young coast redwood-Douglas-fir forests. Forecasts for this region predict rising temperatures, a greater frequency of large storm events, and reductions in summer fog and autumn precipitation (Gonzalez 2015), With so much uncertainty surrounding forest drought vulnerability, especially in wetter environments (Allen et al. 2015), and with 95% of the old-growth redwood forests harvested, the need to understand forest response to climate and drought is paramount. If we want to develop effective restoration projects in these altered and oftentimes degraded coast redwood-Douglas-fir forests, restoration that reduces local competition must be considered.

This research suggests that tree-level competition is a major influence on tree growth and tree drought resistance in young coast redwood and Douglas-fir forests, and highlights levels of competition when trees begin to show low drought resistance. These findings can inform stand and individual tree-level growth models as well as improve

predictive models that assess forest climate vulnerability. They can also aid managers in designing restoration that promotes forest resistance and resilience to climate induced disturbance, by identify key levels of competition that promote positive growth in response to climate variables and drought conditions. With the escalating threat of climate change on the horizon, land managers and conservationists are charged with pioneering new frameworks for forest stewardship and conservation; frameworks that promote necessary resilience while having the ability to adapt to shifting conditions.

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