DROUGHT RESPONSES ACROSS DIVERSE CONIFER SPECIES, HABITATS, AND COMPETITIVE GRADIENTS IN NORTHERN CALIFORNIA

By

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ABSTRACT

DROUGHT RESPONSES ACROSS DIVERSE CONIFER SPECIES, HABITATS, AND COMPETITIVE GRADIENTS IN NORTHERN CALIFORNIA

Gabriel Roletti

Frequent and intense drought events are rapidly altering stand dynamics in western North American forests. Climate, competition, and site characteristics can affect the growth responses of individual trees to drought stress. The ecological and geographical diversity of northern California provides a unique opportunity to measure these responses across species, habitat types, and levels of competitive pressure. This study used dendrochronological techniques and linear mixed-effects models to assess growth responses to drought in four montane and two coastal conifer species across 54 study sites (nine sites per species and 540 trees total) in northern California. Growth was evaluated from 2002-2018 and the drought period was from 2013-2015. There were significant differences among species and environments (coastal or montane) in growth, drought resistance and resilience, and annual latewood proportion. Growth in montane species was generally positively correlated with moisture availability (Palmer Drought Severity Index) and negatively correlated with competitive pressure. The four montane species maintained relatively stable drought resistance, resilience, and latewood proportion across the study period. In contrast, growth in the two coastal species was influenced more by tree size and crown ratio than moisture availability or competition.

As the 2013-2015 drought proceeded, coastal species showed marked reductions in drought resistance and resilience and increases in latewood proportion. The six focal species endured this drought in northern California with reasonably high resistance and resilience. However, the lower resistance observed in coastal species suggests that they may be at risk for increased stress and mortality in the event of more severe, prolonged, and/or frequent droughts.

ACKNOWLEDGEMENTS

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Maidu tribes. I hope this study can contribute to the long-standing ecological knowledge that these communities possess. Thanks to the many people in the National Park Service, California State Parks, the U.S. Forest Service, Humboldt Wildlife Refuge, and the City of Arcata who granted us access to study sites on land under their purvey. Finally, I would like to thank Sarah Aguiar, Perris Alfonzo, Sara Bandali, Asher Budnik, Ian Conway, Jeremy Dustin, Maeve Flynn, Gabriel Goff, Rosalio Gonzalez, Elizabeth Hinojosa, Sophia Lemmo, Suzanne Melendez, Diana Orozco, Brigitte Price, Ashley Shannon, and Colleen Smith for their incredible fortitude and focus during field and lab work; this project would not be possible without you.

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INTRODUCTION

Extreme climate events (e.g., drought), fire, pests, and pathogens have significant effects on forest resilience (Allen et al., 2015; Asner et al., 2015; Reyer et al., 2015; DeSiervo et al., 2018). The frequency and intensity of these types of extreme events are projected to increase along with temperature and water stress throughout many forest regions (Reyer et al., 2015; IPCC, 2018). In particular, the prevalence and duration of drought is expected to increase widely throughout temperate forests, especially in wet ecosystems where prolonged water stress is uncommon (Zang et al., 2014; Martínez-Vilalta & Lloret, 2016; Martin-Benito et al., 2018). More frequent and intense drought events will likely continue to drive tree mortality (van Mantgem & Stephenson, 2007; Allen et al., 2010), which has been underestimated across many forest systems worldwide (Allen et al., 2015).

Drought responses are affected by interactions among competition, forest and site conditions, and exogenous influences such as climate, disturbance, and land management. Understanding drought response requires knowledge of the physiological drivers of tree growth. Xylem water transport, carbon assimilation, and allocation of carbon as non-structural carbohydrates (NSC) are the primary endogenous mechanisms that dictate growth responses to drought (McDowell et al., 2011; Adams et al., 2017; Choat et al., 2018). On a global scale, hydraulic failure is the predominant force contributing to reduced growth and mortality (Anderegg et al., 2016), but the creation and use of NSCs is also critical to drought resistance of conifers (Adams et al., 2017). Carbon balance and hydraulic function are not mutually exclusive mortality mechanisms, as they are often coupled through a feedback loop in which hampered xylem conductivity negatively affects NSC transport and shifts resource allocation towards metabolism and defense instead of growth (McDowell et al., 2008; McDowell et al., 2011). Declining xylem production further reduces hydraulic function as water becomes more limited during drought, decreasing water potential and increasing cavitation within tree vascular tissues. Water stress and impaired hydraulic conductivity prompt some conifer species to increase stomatal closure, reducing photosynthetic carbon assimilation. Carbon starvation then becomes more likely as respiration and metabolism continue to deplete limited NSCs. The predisposition of conifers to hydraulic failure or carbon starvation varies by species (Gessler et al., 2018), making the exact physiological cause of growth reduction difficult to pinpoint. While hydraulic function and carbon assimilation are the main influences on growth, drought response depends on a series of interactions among numerous variables (Farooq et al., 2009). Tree characteristics such as size and crown ratio (percentage of living crown) can also affect drought response in conifers. Tree size influences the capacity for NSC production and accumulation (Stephenson et al., 2014), which provides metabolic energy reserves that can increase drought resistance (Dietze et al., 2014; Adams et al., 2017). Larger crown ratios are associated with increased vigor and photosynthetic capacity (Sprinz and Burkhart 1987, Hasenauer and Monserud 1996; Kramer et al., 2018), which may improve growth during climate stress (Kerhoulas et al., 2013).

Annual Tree Growth

Tree rings are a reliable integrative indicator of tree stress (Oliver and Larson 1996) that are widely used as a proxy to measure tree responses to climate (Lloret et al., 2011; Vaganov et al., 2011). Secondary growth is a low priority compared to metabolism and defense during a stress event (Savidge, 2003), meaning trees produce wider annual rings during optimal climatic conditions and narrower rings during less optimal climatic conditions. Because cellular processes in the vascular cambium are directly limited by climate (Farooq et al., 2009; Vaganov et al., 2011), drought stress can reduce the rate of xylem cell expansion and thickening (Balducci et al., 2016) to ultimately hamper stem growth.

Analyzing intra-annual variability in annual growth rings (earlywood and latewood) can provide information about how seasonal climate affects growth (Domec and Garter, 2002; Eilmann eat al., 2013; Camarero et al., 2020). Earlywood xylem consists of wider conduits bounded with comparatively thinner cell walls, whereas latewood xylem conduits are narrower and are supported by significantly thicker cell walls (Speer, 2010). Latewood, due to these narrower xylem conduits, has less hydraulic capacity and higher resistance to cavitation during water stress (Domec and Garter, 2002). Xylem production is initiated, in part, by the increase in temperature associated with the onset of spring and can continue until fall or later (Speer, 2010). Current spring and previous early winter temperature and precipitation are often correlated with earlywood growth (Lebourgeois, 2000; Jiang et al., 2017; Gao et al., 2018). The majority of latewood formation often occurs in mid-summer and is usually correlated with summer precipitation, although the timing and duration of latewood formation varies by species (e.g., Lebourgeois, 2000; Martin-Benito et al., 2008, Vieira et al., 2009; Speer, 2010; Gao et al., 2018). Summer droughts typically decrease latewood production and reduce the latewood proportion (LWP) of an annual ring (Meko & Baisan 2001), whereas spring or winter droughts decrease earlywood production and can increase LWP.

Tree Responses to Competition

Competition is one of the most dominant influences on forest composition, structure, and stand dynamics (e.g., Das et al., 2009; Carnwath & Nelson, 2016), often outweighing climatic effects in large-scale analyses (Linares et al., 2010; Clark et al., 2014; Ford et al., 2017; Gleason et al., 2017). Competition is an interaction between neighboring flora due to the use of shared limiting resources that can lead to reductions in growth, recruitment, and survival (Das et al., 2009; Carnwath & Nelson, 2016). High levels of competition influence resistance and resilience of trees to climate stress and affect the adaptive capacity of forests (Linares et al., 2010; Sanchez-Salguero et al., 2015). Resistance is the ability to remain ecologically unchanged during disturbance, whereas resilience is the ability to reach pre-disturbance levels of performance following disturbance (Lloret et al., 2011). Species-specific responses to competitive pressure vary (Das et al., 2011; Clark et al., 2014; Ford et al., 2017), with certain species having greater abilities to withstand environmental stressors in the face of competition than others. Intra-specific competition may commonly affect individual trees more than inter-specific competition because conspecific trees compete for a similar suite of growth-limiting resources (Das et al., 2011).

Understanding how competition influences drought response in individual trees across different habitats (e.g., wet, moderate, dry) is important to predict how forests will change in the future because this interaction may cause unexpectedly severe consequences (Linares et al., 2010; Clark et al., 2016; Young et al., 2017). Since individual trees can respond to climate differently depending on their competitive environment (Clark et al., 2016; Ford et al., 2017), sensitivity to drought stress tends to vary across gradients of competition (Carnwath and Nelson, 2016). Competition often has a stronger negative effect on growth than climate in wet habitats or during wetter years. In arid or traditionally water-stressed habitats moisture stress can replace competition as the predominant control on growth (Sanchez-Salguero et al., 2015; Carnwath and Nelson, 2016). While trees can withstand many seasons of low growth in conjunction with stressors like increased competition (Cailleret et al., 2017), this physiological strain can predispose them to pest and pathogen attacks that can ultimately result in mortality (e.g., DeSiervo et al., 2018). Thus, in wet to semi-arid ecoregions, competition can amplify drought-induced mortality (Moore et al., 2016) such that this interaction has the potential to drastically alter the distribution of tree species (Benito-Garzón et al., 2013; McDowell & Allen, 2015).

Northern California Tree Responses to Disturbance

In California, the 2012-2016 drought was the most severe in the last 1200 years. Drought conditions in California have persisted (i.e., 2020-2022) (Mankin et al., 2021), and are predicted to continue in the future. Overall precipitation, runoff, and summer top-level soil moisture are projected to fall below historical medians for the next 20 years (Pierce et al., 2018), while temperatures could increase 1.5-3.0 ℃ by mid-century (Micheli et al., 2018). Although research in southern California and the southwestern U.S. demonstrates that abiotic (e.g., fire) and biotic (e.g., insect outbreaks) stressors combined with increasing drought affect forest resilience and tree mortality (Moore et al., 2016; Stephens et al., 2018; Fettig et al., 2019), it is less clear how the biodiverse forests throughout northern California have responded to similar stressors. The few studies that do address forest resilience and mortality in northern California occur in particular stand types (e.g., Vernon et al. 2018, Wenderott et al. 2022) or are broad scale remote sensing studies across all forest types (Young et al., 2017; Golden and Bales, 2019).

Throughout northern California and the Pacific West, climate change is increasing the likelihood of extreme drought conditions (Diffenbaugh et al. 2015, Williams et al. 2015) and amplifying the existing Mediterranean-type seasonality, leading to more abbreviated wet seasons, longer dry seasons, and more intense and frequent storms (Swain et al., 2018). Although average temperatures across northern California are predicted to increase 2.0-2.5 °C by 2070 (Garfin et al., 2014; Micheli et al., 2018), interior regions will likely continue to experience a disproportionate amount of warming compared to coastal areas. Additionally, precipitation has become more variable across northern California in the last 10 years, and this variability is projected to increase in the coming decades (Swain et al., 2018). While the total average precipitation across the entire region is likely to increase, the majority of this precipitation will fall on the mountains of the North Coast, leaving interior montane habitats moisture-deprived. Higher temperatures and reduced inland precipitation will diminish snowpack, decrease dry season streamflow and run-off, elevate soil aridity, and increase water stress on vegetation (Grantham, 2018). These increases in inland temperature and precipitation variability raise the probability of enhanced drought magnitude and duration in northern California (Diffenbaugh et al., 2015; Wehner et al., 2017).

Thus, an improved understanding of how drought and competition interact with climate to affect tree growth, resistance, and resilience is essential to inform adaptive forest management plans (Johnstone et al., 2016). To date, these interactions have been measured at individual tree or neighborhood scales in very few locations in northern California (e.g., DeSiervo et al., 2018, Vernon et al., 2018), and no investigations have been carried out across a wide range of conifer species. The Klamath Mountains and surrounding forested areas were renowned climate refugia during the Pleistocene that provided opportunities for an incredibly diverse range of species, including many endemics, to persist during shifts in climate (Kauffmann, 2012; Olson et al., 2012). The protection and informed management of these areas is critical for their conservation in the face of climate change. The goal of this study was therefore to examine how climate and competition interacted to influence conifer responses to the recent drought in northern California. Six conifer species of varying abundance and geographic distribution (Table 1) were selected to evaluate these responses across wet, moderate, and dry habitats. Results will help determine how northern California forests may change as drought becomes more common and severe. The specific question and hypotheses investigated in this study were:

1. How do climate, competition, and site and tree characteristics influence conifer growth?
    a. Annual growth is positively related to annual moisture availability because water is often a limiting factor of diameter growth. Moisture has a greater effect on montane conifer growth than in coastal species because coastal sites are generally less water-limited.
    b. Competition has a stronger negative effect on growth than climate due to a greater reduction in resource availability. This trend is stronger in montane species than coastal species because montane species are more acclimated to reduced moisture inputs.
    c. Growth is positively related to long-term moisture availability because water is less limiting in wetter habitats. This relationship varies by species.
    d. Growth varies among conifer species and is greater in larger trees compared to smaller trees because different species are sensitive to different influences and because larger trees have larger leaf areas, deeper roots, and greater storage capacity.

2. How do drought resistance and resilience, and latewood proportion vary among conifer species and across successive years of drought?
    a. Drought resistance and resilience will vary among species, will be lowest in coastal species due to their acclimation to moister conditions, and will decrease with drought duration as hydraulic damage accumulates and carbon reserves are depleted.
    b. Latewood proportion (LWP) will vary among species and will increase during drought; this drought response will be most pronounced in wet habitats, as increased production of latewood is a physiological defense against hydraulic failure associated with dry periods, and dry periods are relatively rare in traditionally wet habitats.

Table 1. Abundance, range, and distribution of focal conifer species. Abundance includes: Common = widespread; Uncommon = not widespread, restricted, and rarely dominant. Regional range includes: All = montane and coastal; Coastal = within 50 km of coast; Montane = generally high elevation. Adapted from Table 2.2 in Kauffmann, 2012. Abbreviations: NW = northwest; NA = North America

Common Name	**Scientific Name**	**Abundance**	**Regional Range**	**Distribution**
Shasta fir	*Abies magnifica* var. *shastensis*	Common	Montane	Endemic
Brewer spruce	*Picea breweriana*	Uncommon	Montane	Endemic
Sitka spruce	*Picea sitchensis*	Uncommon	Coastal	Pacific NW
Sugar pine	*Pinus lambertiana*	Common	All	California
Western white pine	*Pinus monticola*	Uncommon	Montane	Western NA
Western hemlock	*Tsuga heterophylla*	Common	Coastal	Pacific NW

METHODS

Study Area and Design

The study area is located in northern California and includes the Klamath Mountain and the North Coast regions of the state. This assemblage of mountain ranges is bounded by temperate coniferous forests of the Cascades to the north, the Modoc Plateau to the east, and the Sierra Nevada to the southeast. A series of transverse coastal mountains called the North Coast Range make up the western-most portion of the study area, which is ultimately bordered by the Pacific Ocean (Kauffmann, 2012). This complex regional topography combined with a strong west-east climate gradient creates highly variable local temperature and precipitation. The North Coast Range receives 1400 mm of annual precipitation on average (1981-2010), with the majority falling on the coastal regions (Grantham, 2018). The regional climate exhibits a distinctive, Mediterranean-type seasonality in which most precipitation falls between November and April, followed by a prolonged dry season from May through October. Precipitation decreases and summer temperatures and aridity increase from the Oregon border southward to the Central Valley and eastward from the North Coast Ranges to the Cascades. In northern California, coastal temperatures range from 0 to 30 °C, whereas interior temperatures often fall below 0 °C in the winter and exceed 35°C in the summer (Grantham, 2018). This variation of climatic and geographic features makes northern California an excellent microcosm of many of the habitats in which conifers exist throughout the world. The unique geography of this region creates varying microclimates that act as climate refugia to support more than 3,000 species of vascular plants, including 38 species from 13 genera of conifers (Kauffmann, 2012; Olson, 2012). This botanical diversity makes the region one of the most ecologically diverse landscapes in the world and provides an excellent natural laboratory in which to investigate drought responses for a variety of conifer species.

Site selection

The sampling protocol consisted of three replicates of three climate habitats (wet, moderate, dry) for six conifer species (Table 1): *Abies magnifica* var. *shastensis* Lemmon, *Picea breweriana* S. Watson, *Picea sitchensis* (Bong.) Carriere, *Pinus lambertiana* Douglas, *Pinus monitcola* Douglas ex. D. Don, and *Tsuga heterophylla* (Raf.) Sarg. The CalFlora botanical database (www.calflora.org) was used to systematically identify known locations of specific focal species within each species' geographic range in northern California (Kauffmann 2012). CalFlora locations with a slope of less than 30° that were within 3.2 km of a road were selected to ensure accessibility by using a USGS digital elevation model (https://viewer.nationalmap.gov/basic/) and road layer in ArcGIS Pro (ESRI, 2019). The CalFire (https://frap.fire.ca.gov/mapping/gis-data) fire history layer was overlaid on each of the selected locations to remove locations with a record of fire activity during the 20th or 21st century. A combination of aerial imagery and in-situ inspection was used to avoid locations with obvious signs of undocumented, recent disturbances (e.g., fire, logging, widespread mortality). Habitat type (wet, moderate, or dry) was defined by the 30-year (1981-2010; www.prism.oregonstate.edu) mean annual precipitation at each of the selected CalFlora locations. For each species, habitat type was designated by dividing the range of 30-year precipitation means across all CalFlora points into thirds representing “relative” wet, moderate, and dry conditions. Lastly, locations expressing a 2014 and 2015 Palmer Drought Severity Index (PDSI) value of less than -2 were considered drought-affected and considered for sampling (http://www.climatologylab.org/gridmet.html). PDSI is a standardized index ranging from -10 (extremely dry) to 10 (extremely wet) that incorporates temperature and precipitation measurements with soil water balance information to estimate drought intensity relative to long-term average conditions at a particular site (Palmer, 1965). The lowest available PDSI value did not meet the -2 PDSI threshold in 2014 at ten sites. In these cases, the locations with the lowest PDSI values were selected, which were all between -1 and -2. PDSI values in 2015 were all less than -2. Michael Kauffmann, a locally renowned northern California conifer expert and natural historian (e.g., Kauffmann 2012), vetted locations and provided alternative locations when necessary (e.g., when CalFlora locations had an undocumented fire or when tree harvesting activity limited sampling).

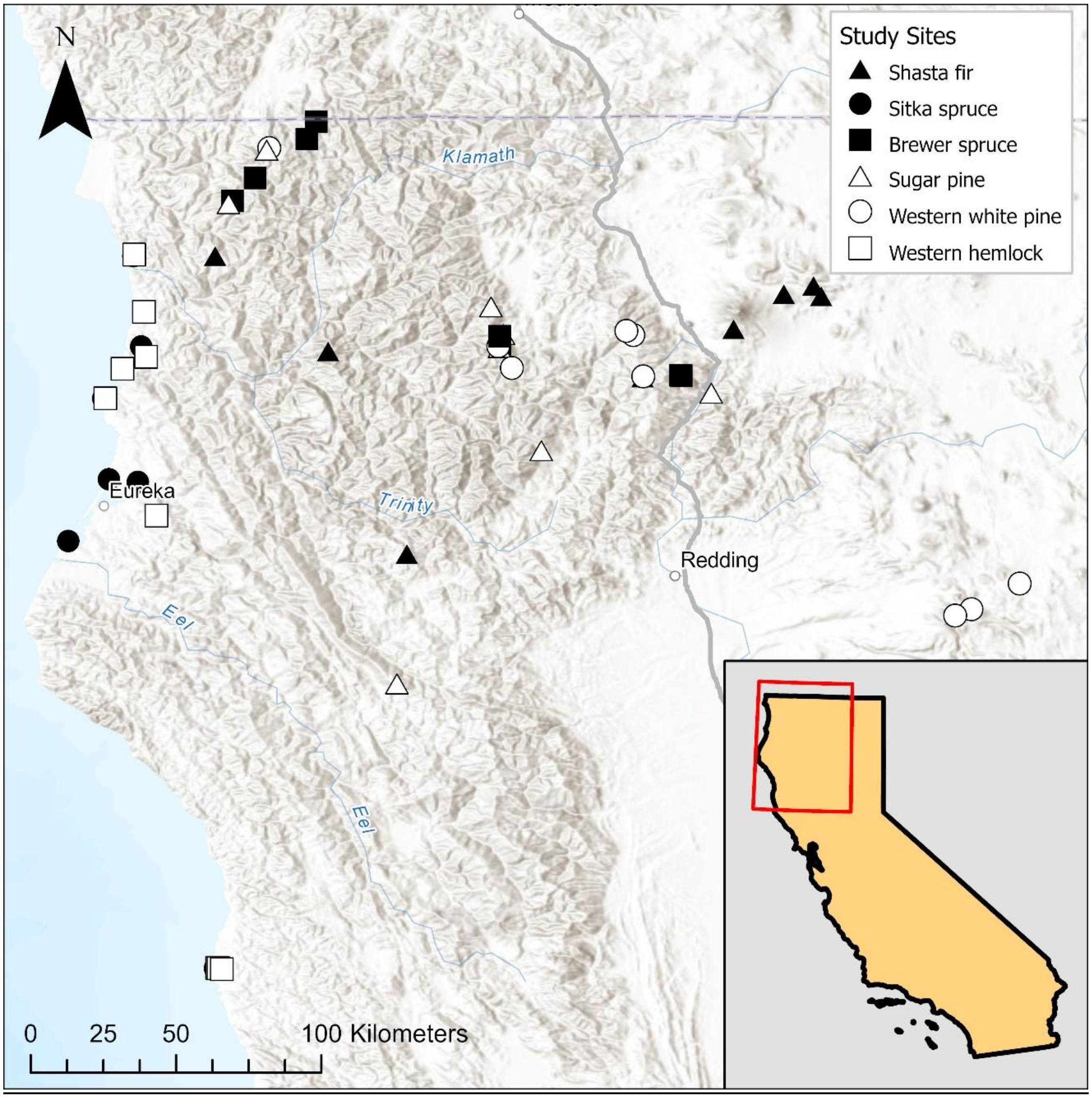

Figure 1. Map of the study area. Species-specific labels denote locations of study sites across northern California. Map made with ArcGIS Pro (ESRI, 2021).

Field sampling

After identifying a large set of suitable possibilities using the above criteria, 54 locations were selected for sampling the six focal species, each with three replicates of dry, moderate, and wet habitats. The GPS coordinate of each CalFlora location was used as a target sampling point and were not randomly selected. At each location, the 10 closest dominant or co-dominant trees were selected for the species of interest. Trees with intermediate canopy positions were only selected when necessary for western hemlock and Brewer spruce because of the rarity of occurrences as dominant or co-dominant. Focal trees were chosen at a minimum of 20 m apart from one another. When the target species of a particular site was unusually scarce, a minimum of 15 m was used to ensure that 10 individual trees could be sampled. A buffer of 30 m from paved roads and 10 m from trails was maintained. Trees with obvious damage or disease were not selected for sampling. Trees within 30 m of active watercourses, seeps, or drainages were also avoided.

Two cores were taken from each focal tree 90° apart from one another at or near breast height (1.37 m). Core height, bole diameter at core height, and bark thickness measurements were taken for each core. A total of 540 trees were cored across all six species, generating 1,080 individual cores. Tree-level characteristics of each focal tree were collected including species, diameter at breast height (DBH), crown ratio, tree competition (see below), and canopy position (dominant, co-dominant, intermediate).

Data Processing and Analyses

Tree Growth

The core samples were prepared, sanded, and analyzed using standard dendrochronological techniques (Speer 2010). For the growth analysis, measurements of annual ring widths (RW), earlywood (EW) and latewood (LW) widths, and latewood proportion (LWP = LW/RW × 100) were measured using WinDendro software (Regent Instruments Inc., Québec, Canada). All cores were statistically cross-dated using Cofecha (Holmes, 1984). Raw RW values were converted to basal area increment (BAI) using bark thicknesses measured in the field for each focal tree in the dplR package in R (Bunn, 2008)(Figure 2). Mean BAI and LWP for each species are shown in appendix A.

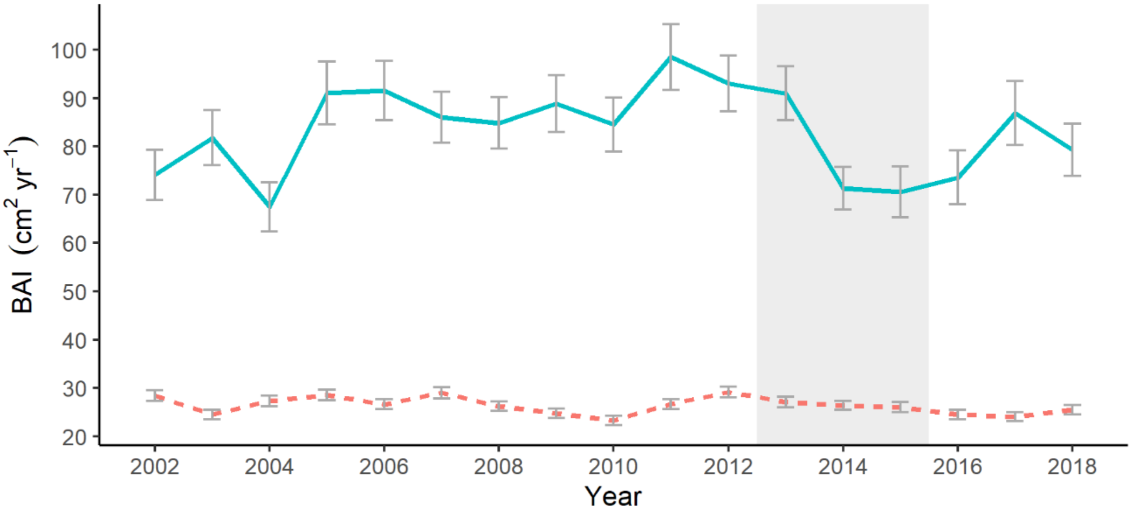

Figure 2. Mean (± SE) annual basal area increment (BAI) across all study sites (*n* = 54) between 2002 and 2018. Study sites are divided into montane (dashed line) and coastal (solid line) environments. Drought period (2013-2015) is shaded grey.

Table 2. Number of trees per species, diameter at breast height (DBH), total Hegyi index, annual basal area increment (BAI), growth-based drought resistance and resilience (DRR), and latewood proportion (LWP). DRR and LWP values are based on 2013-2015 drought years and 2016-2018 post-drought years, respectively. Values reported as mean ± SE.

Species	**Trees (*n*)**	**DBH (cm)**	**Hegyi**	**BAI (cm^2)**	**DRR**	**LWP (%)**
Montane						
Shasta fir	90	80 ± 1	2.0 ± 0.2	33 ± 0.5	0.92 ± 0.01	12 ± 0.2
Brewer spruce	90	56 ± 1	2.4 ± 0.3	23 ± 0.4	1.02 ± 0.01	15 ± 0.3
Sugar pine	90	92 ± 1	1.4 ± 0.2	29 ± 0.5	1.04 ± 0.01	12 ± 0.3
Western white pine	90	73 ± 1	2.3 ± 0.2	21 ± 0.4	0.99 ± 0.01	13 ± 0.4
Coastal						
Sitka spruce	87	110 ± 2	0.9 ± 0.1	117 ± 1.9	0.91 ± 0.02	10 ± 0.4
Western hemlock	79	74 ± 1	1.3 ± 0.2	45 ± 1.0	0.84 ± 0.02	14 ± 0.5

Climate

To explore relationships between tree growth (BAI) and climate at different habitat types (dry to wet locations for each species based on 30-year precipitation means), monthly climate data were extracted from the TerraClimate database (http://www.climatologylab.org/terraclimate.html) using the coordinates of the first focal tree at each site. Monthly climate data were then averaged by calendar year and the following climate variables were evaluated: Annual mean precipitation (PPT), annual average minimum temperature (°C; TMN), and annual average maximum temperature (°C; TMX). Mean water-year precipitation (PPT_WY, previous year October through current year September), and annual calendar year PDSI values were also evaluated as measures of water availability and drought (Figure 2). One-year lagged, two-year lagged, and three-year lagged PDSI values were also investigated to account for potential lagged responses to moisture availability. The TerraClimate model accounts for variation in slope and aspect across sites and uses a spatial resolution of 4 km. Variables that were highly correlated with growth were included in the model selection process.

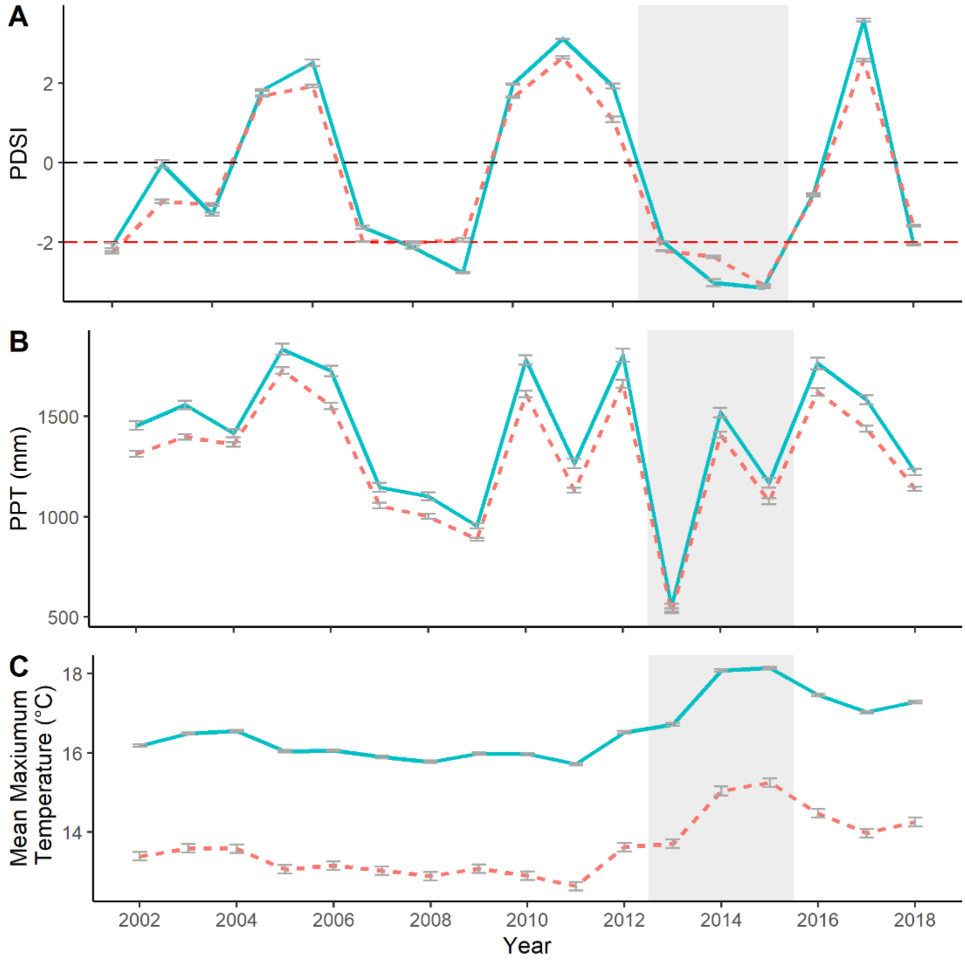

Figure 3. Time series (2002-2018) showing annual mean (± SE) Palmer Drought Severity Index (PDSI) (A), precipitation (PPT) (B), and basal area increment (BAI) (C) experienced at both coastal (solid line) and montane environments (dashed line). Drought period (2013-2015) is shaded grey; in (A), a dashed red line at PDSI -2 represents the drought threshold used.

Tree and Site Characteristics

Several variables were evaluated to explore relationships between growth (BAI) and tree and site characteristics. Diameter at breast height (DBH), canopy position (dominant, co-dominant, or intermediate), and canopy competition (1-4 based on amount surrounding canopy trees directly overlap the crown of the focal tree) was recorded in the field for each individual tree. Heat load index values were generated for each site location to account for potential variation in annual direct incident solar radiation (R-package *spatialEco*; McCune and Keon, 2002). Finally, monthly values of snow water equivalent (TerraClimate Database) were averaged by calendar year to investigate the effect of snow pack on growth at each site.

Drought resistance and resilience

The study area experienced a relatively drought-free period from 2009-2012 (PDSI > -1), a severe drought (defined in this study by average PDSI values of $\leq$ -2 across all sites) from 2013-2015, and another relatively drought-free period from 2016-2018 (Figure 3). Mean annual drought resistance was calculated for each focal tree by dividing the BAI of each drought year by the 4-year (2009-2012) mean pre-drought BAI. Average drought resistance was also calculated for each focal tree by dividing the mean drought BAI (2013-2015) by the 4-year pre-drought mean BAI. Resilience for each focal tree was calculated by dividing annual post-drought BAI values (2016-2018) by the same 4-year pre-drought mean BAI.

Competition

A competition neighborhood includes all trees within a radius that actively influence the growth of a focal tree. For conifers, this distance is accepted to be between 10 and 20 m (e.g., Das et al., 2011; Vernon et al., 2017). In this study, the Hegyi index was calculated to evaluate the local competitive pressure within 10 m of each focal tree (Hegyi, 1974) using the following the equation:

$$Hegyi_t = \sum_{i=1}^{n} \frac{DBH_i}{DBH_t} \times \frac{1}{dist_i}$$

where $Hegyi_t$ represents the competitive strain on the focal tree t, DBH_t is the DBH of the focal tree, DBH_i is the DBH of each competitor tree i, and dist_i is the distance between them, summed for all competitor trees within a 10 m radius. The Hegyi index was calculated for each tree in three different ways: Intra-specific competition, inter-specific competition, and total competition (Figure 4).

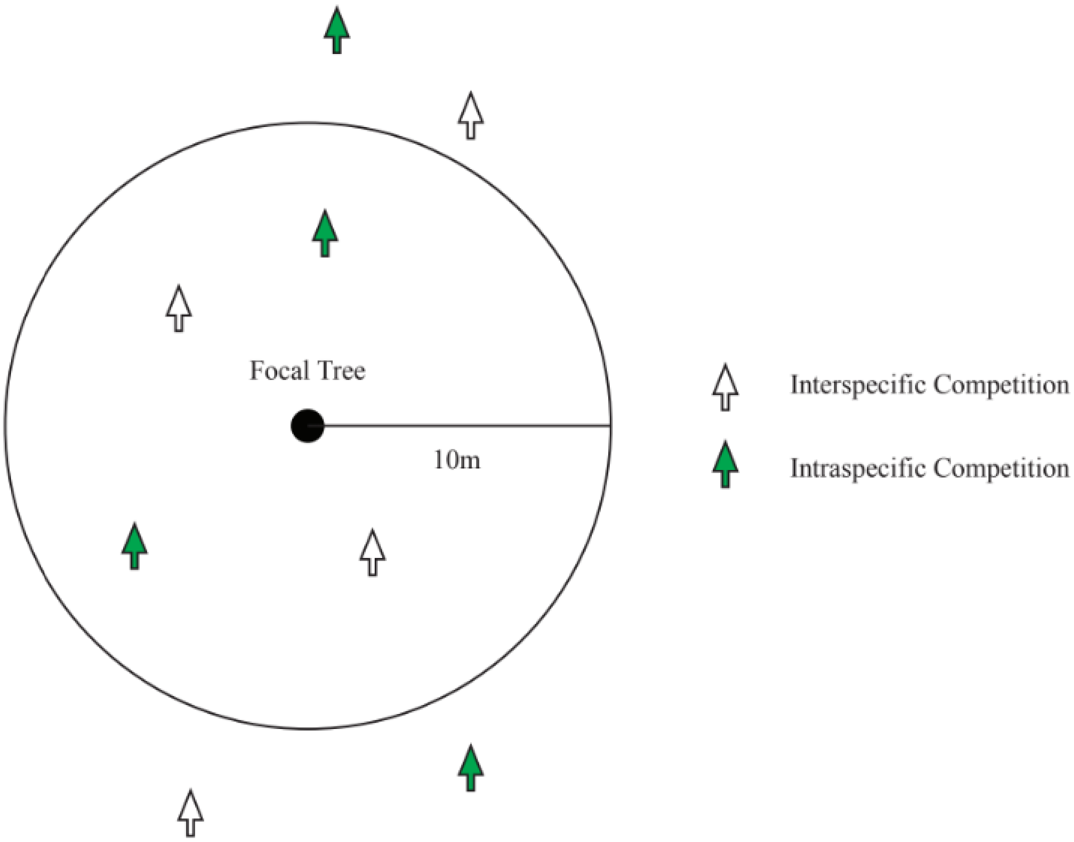

Figure 4. Layout of a hypothetical plot within one of the 54 sites. Dark colors represent interspecific competitor trees larger than 5 cm DBH and light colors represent intraspecific competitors larger 5 cm DBH. The linear distance and DBH of all qualified competitors within a 10 m radius of the focal trees were measured.

Statistical analyses

Linear mixed-effects models (LME) created with the *glmmTMB* package in R were used to evaluate both research questions (Brooks et al., 2017; R Core Team 2019). For all models, numeric predictor variables were standardized by subtracting the mean and dividing by two standard deviations to aid in interpretation and comparison of model coefficients (Gelman, 2008). Full (all variables included) and selected “best” models were evaluated for homogeneity of variance by viewing plots of scaled residuals and for distribution fit by viewing quantile-quantile plots (R-package *DHARMa*; Hartig, 2022). Multicollinearity was checked and best models had variance inflation factors of less than 2. The grouping of trees within sites was addressed in all models by using a nested random effect of tree within site to account for variation in site condition and in the individuals measured.

Species-specific and pooled environment (coastal and montane) LME models (gamma distributed with log link) were used to evaluate the effects of annual water availability (PDSI), other significant climate variables (e.g., TMN, TMX, PPT, PPT_WY) competition, environment (coastal v. montane), and site and focal tree characteristics on BAI. The response variable, BAI, was fit using the R-package *glmmTMB* (Brooks et al., 2017). To account for temporal autocorrelation associated with repeated measurements, a first-order autocorrelation (AR1) structure was included in each growth model because it was the simplest autocorrelation structure that also improved Akaike Information Criterion (AIC). Fixed-effects structure was determined by comparing the AIC of intercept-only models to individual models of each predictor (Appendix A). All predictors that explained BAI better than the corresponding intercept-only models were included in an all-subsets regression (R-package *MuMIn,* Barton, 2022*)* that prevented the combination of variables with high intercorrelation (i.e, PDSI and TMAX, $r > 0.30$) and ranked remaining variable combinations by AIC. Backward elimination was then used to sequentially remove remaining effects that were not statistically significant (*p* >0.05). Models with an AIC of at least two less than the next best model were selected (Appendix B). The interaction between competition (Hegyi) and site-level moisture availability (30-year mean precipitation), and the interaction between competition and annual water availability (PDSI), were tested in every final model based on the hypotheses posed in research Question 1.

To evaluate annual drought resistance and drought resilience (DRR) across species and between coastal and montane environments, two separate LME models (Gaussian distribution with a log-link) were created that included drought resistance (2013-2015) and drought resilience (2016-2018) as a response variable with focal tree nested in site as a random effect. Drought resistance and drought resilience were calculated separately (Lloret et al., 2011) and included together in each model. One model used species and year as main effects to assess variation in mean annual DRR among species, and the second model used environment (coastal or montane) and year as main effects to compare mean annual DRR. A third LME model (beta distribution with a log-link) used LWP as a response variable, species and year as fixed effects, and focal tree nested in site as a random effect. Two-way analyses of variance (ANOVA) followed by Tukey's multiple comparison tests confirmed differences in the DRR and LWP values (Packages *emmeans* and *multicomp* in R; Hothorn & Bretz, 2008; Lenth, 2021).

RESULTS

Effects of Competition, Climate, and Site and Tree Characteristics on Growth

Mixed-effects models found meaningful predictors of growth for all species; due to the gamma distribution used, effects < 1 are negative and effects > 1 are positive. For both coastal species (Sitka spruce and western hemlock), growth was positively correlated with PDSI (Figure 5). The best mixed-effects model of Sitka spruce BAI (n = 1,462 tree-rings from 86 trees; $R^2 = 0.14$) included positive effects of crown ratio (effect size = 1.33, $p = 0.04$) and PDSI (effect size = 1.11, $p < 0.0001$). The best mixed-effects model for western hemlock BAI (n = 1,309 tree-rings from 77 trees; $R^2 = 0.10$) included positive effects of DBH (effect size = 1.75, $p < 0.0001$) and two-year-lagged PDSI (effect size = 1.09, $p = 0.002$). The pooled coastal species model (n = 2,771 tree-rings from 163 trees; $R^2 = 0.10$) included positive effects of PDSI (effect size = 1.08, $p < 0.0001$), crown ratio (effect size = 1.25, $p = 0.01$), and DBH (effect size = 1.77, $p < 0.0001$).

For montane species, BAI was positively correlated with two-year-lagged PDSI in all species' models except for sugar pine (Figure 5). BAI was also consistently positively related to crown ratio and negatively related to competition (in three of four montane species). For Shasta fir (n =1,530 rings from 90 trees; $R^2 = 0.12$), the best model included interspecific competition (effect size = 0.67, $p = 0.0012$), two-year-lagged PDSI (effect size = 1.09, $p = 0.0004$), and crown ratio (effect size = 1.29, $p = 0.03$). The best model for Brewer spruce (n = 1,530 rings from 90 trees; $R^2 = 0.14$) included crown ratio (effect size

= 1.47, $p = 0.0018$), two-year-lagged PDSI (effect size = 1.11, $p < 0.0001$), and total competition (effect size = 0.77, $p = 0.02$). For sugar pine ($n = 1{,}530$ rings from 90 trees; $R^2 = 0.04$), the best model included total competition (effect size = 0.76, $p = 0.01$). The best model for western white pine ($n = 1{,}530$ rings from 90 trees; $R^2 = 0.13$) included crown ratio (effect size = 1.65, $p = 0.0003$) and two-year-lagged PDSI (effect size = 1.13, $p < 0.0001$). The pooled montane model did not perform better than an intercept-only model and no further exploration was carried out.

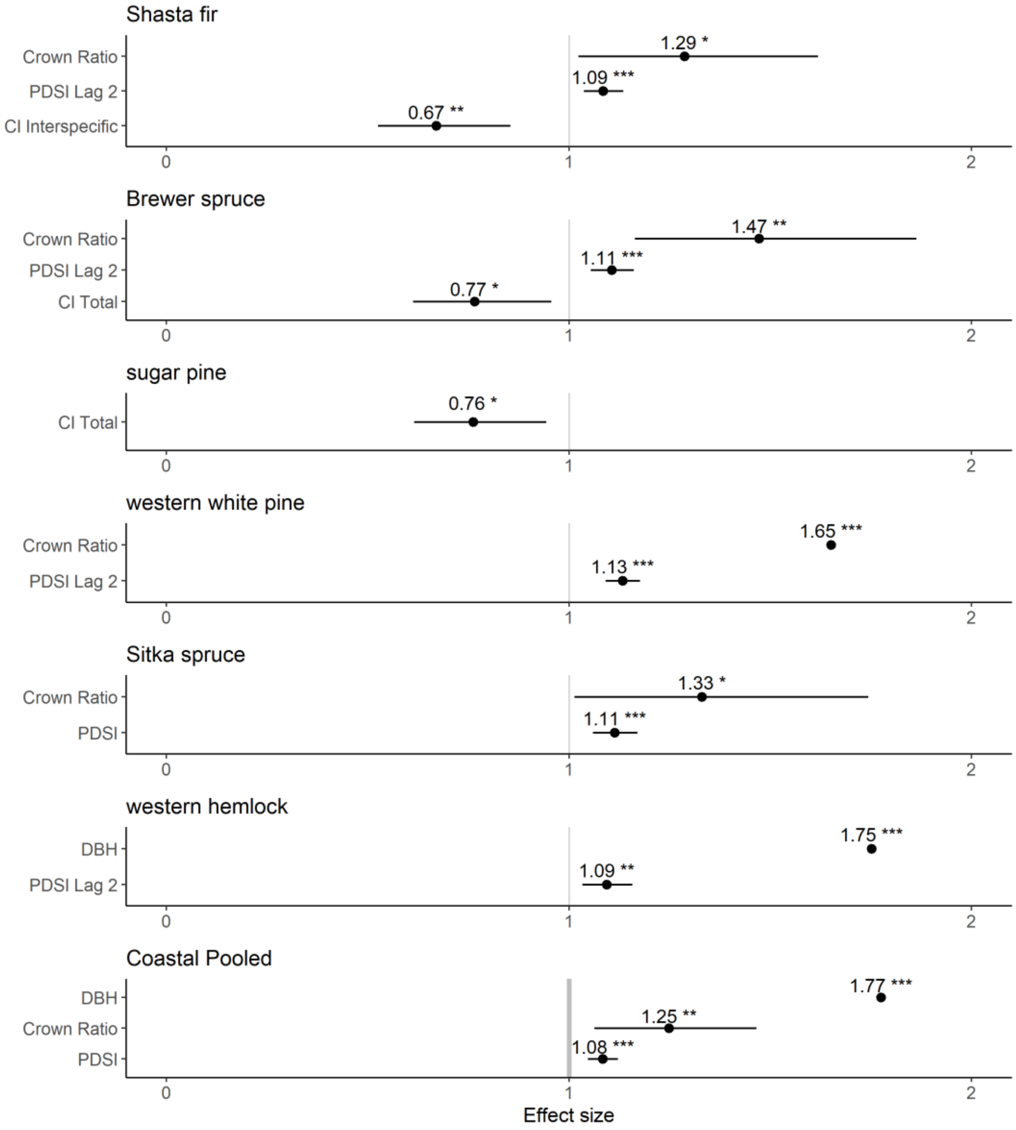

Figure 5. Multiplicative effect size of predictor variables on basal area increment (BAI) in the final generalized linear mixed-effects models for Shasta fir (*n* = 90 trees), Brewer spruce (*n* = 90 trees), western white pine (*n* = 90 trees), sugar pine (*n* = 90 trees), Sitka spruce (*n* = 87 trees), western hemlock (*n* = 77 trees), and the coastal pooled model (*n* = 164 trees, Sitka spruce and western hemlock). Values have been back-transformed 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. Predictor variables include: ratio of live crown (Crown Ratio), Palmer Drought Severity Index (PDSI) and its 2-year lag (PDSI LAG 2), total Hegyi index (CI Total), total interspecific Hegyi index (CI Interspecific), and diameter at breast height (DBH). Bars represent 95% confidence intervals. Asterisks denote significance levels of *p*-values (* < 0.05, ** < 0.01, and *** < 0.001).

Species-level Drought Resistance

Drought resistance during the study period varied among species (Figure 6). In drought years 2014 and 2015, drought resistance of montane species increased significantly more than coastal species. This trend continued in post-drought years 2016 through 2018, with coastal species experiencing decreased resilience compared to montane species (Figures 6 and 7). More specifically, for each coastal species and for the pooled coastal species, resistance significantly decreased in drought years 2014 and 2015 and in post-drought year 2016 and increased in post-drought years 2017 and 2018. In montane species, Shasta fir resistance significantly decreased during the post-drought period. Brewer spruce drought resistance had a decreasing trend, although it did not significantly differ among years. Sugar pine resistance remained relatively constant (1.04 ± 0.05) between 2013 and 2018, with one significant decrease in 2017. Western white pine resistance remained constant between drought years 2013 and 2015, significantly decreased in post-drought years 2016 and 2017, and then significantly increased in 2018 to the highest level (1.10 ± 0.06) measured among all species.

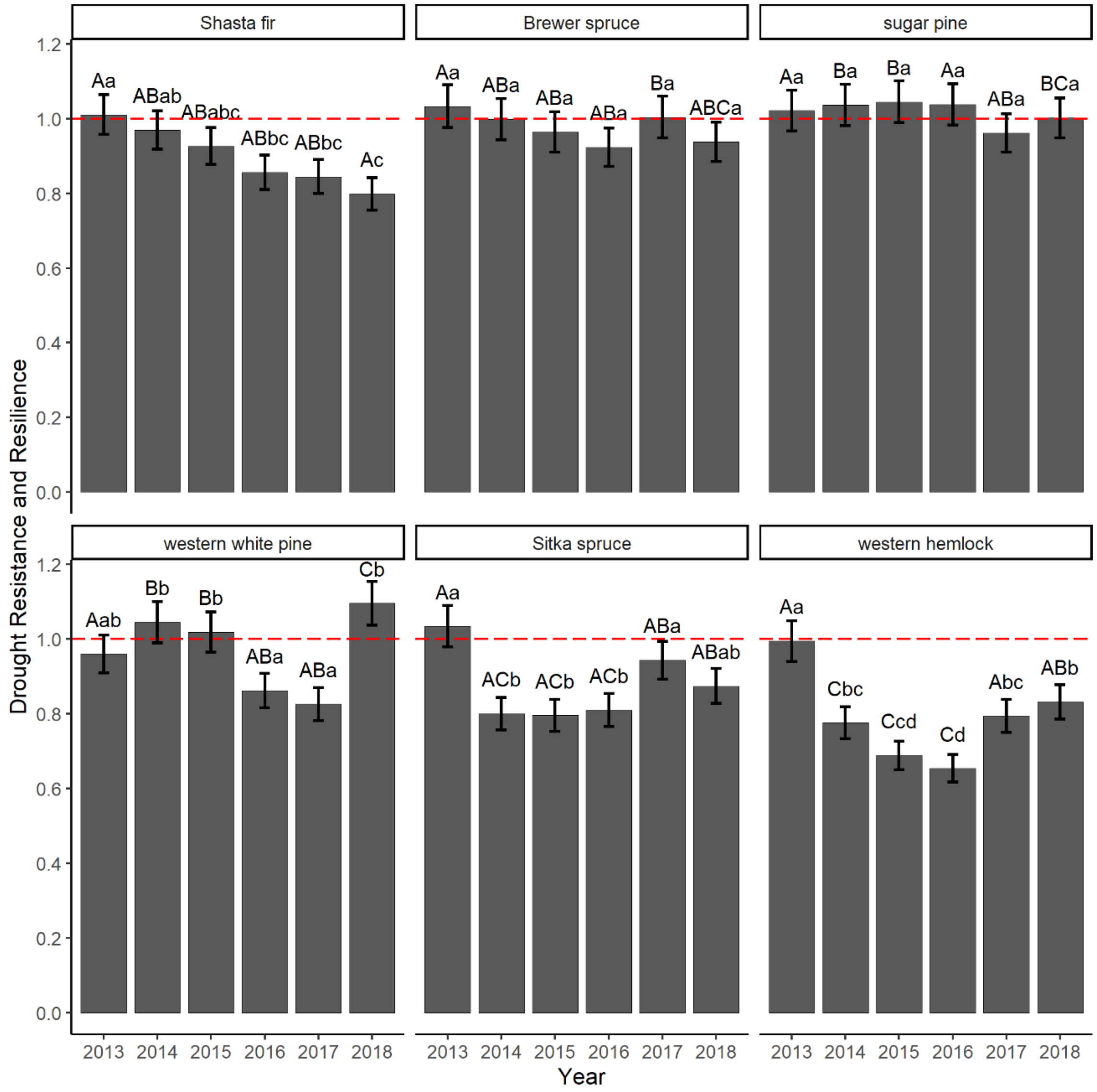

Figure 6. Mean (± SE) annual drought resistance (2013-2015) and resilience (2016-2018) for each focal species. Drought resistance and resilience values > 1 represent greater growth during drought, values < 1 represent lower growth during drought, and values at 1 represent no change in growth during drought compared to the pre-drought period (2009-2012). Within a year, species not sharing uppercase letters are significantly different; within a species, years not sharing lowercase letters are significantly different. The red dashed line at 1 represents no change in growth during or after drought compared to pre-drought.

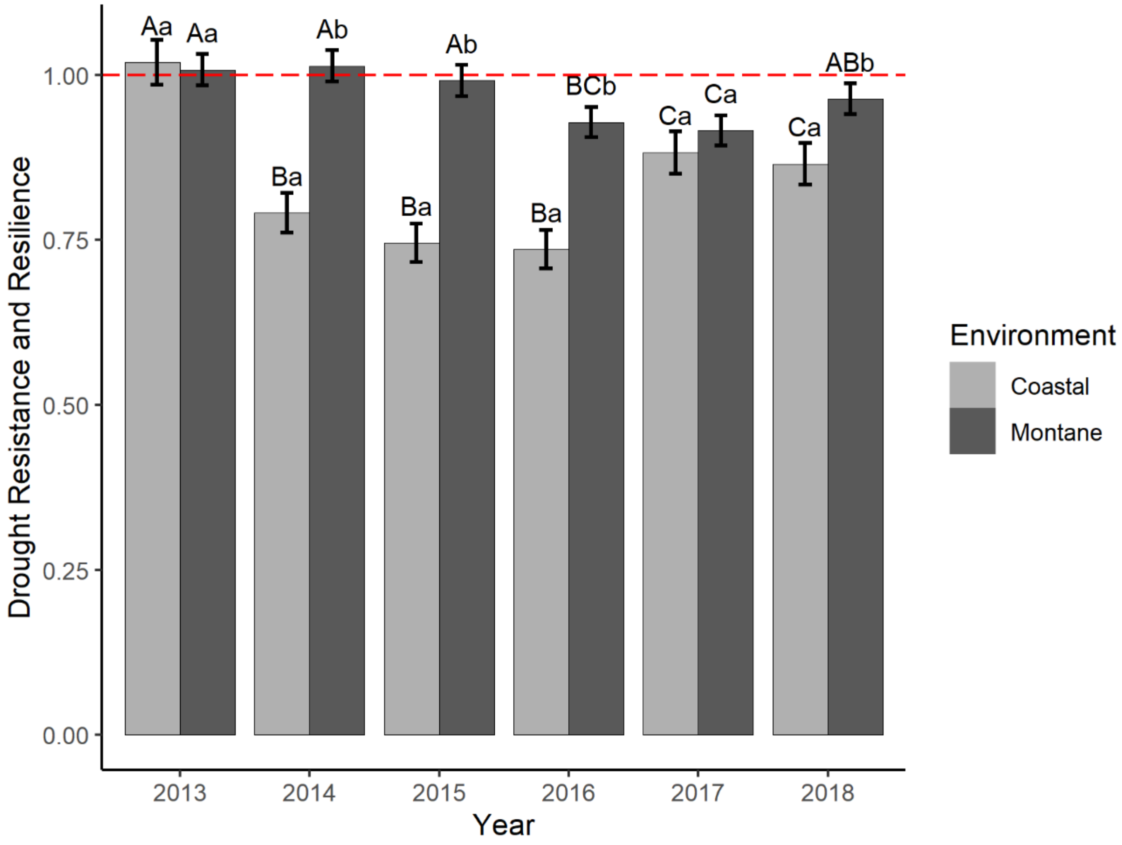

Figure 7. Mean (± SE) annual drought resistance (2013-2015) and resilience (2016-2018) for coastal and montane species. Drought resistance and resilience values > 1 represent greater growth during drought and values < 1 represent lower growth during drought. Within a year, environments not sharing lowercase letters are significantly different; within an environment, years not sharing uppercase letters are significantly different. The red dashed line at 1 represents no change in growth during or after drought compared to pre-drought.

Effect of Drought on Latewood Proportion

There were few annual differences in LWP among species, although Sitka spruce produced significantly less latewood than Brewer spruce throughout the study period (Figure 8). For coastal species, LWP increased during drought (2014 and 2015) and the first post-drought year (2016) compared to the pre-drought period. For montane species, Shasta fir LWP was relatively constant but increased significantly in post-drought year 2018. Brewer spruce LWP increased significantly in 2016 compared to the pre-drought period. Sugar pine LWP decreased significantly in the 2015 drought compared to the post-drought year of 2016. Western white pine LWP showed notable inter-annual variability and different trends than other montane species (i.e., post-drought, increased in 2016 and 2017 and then decreased in 2018).

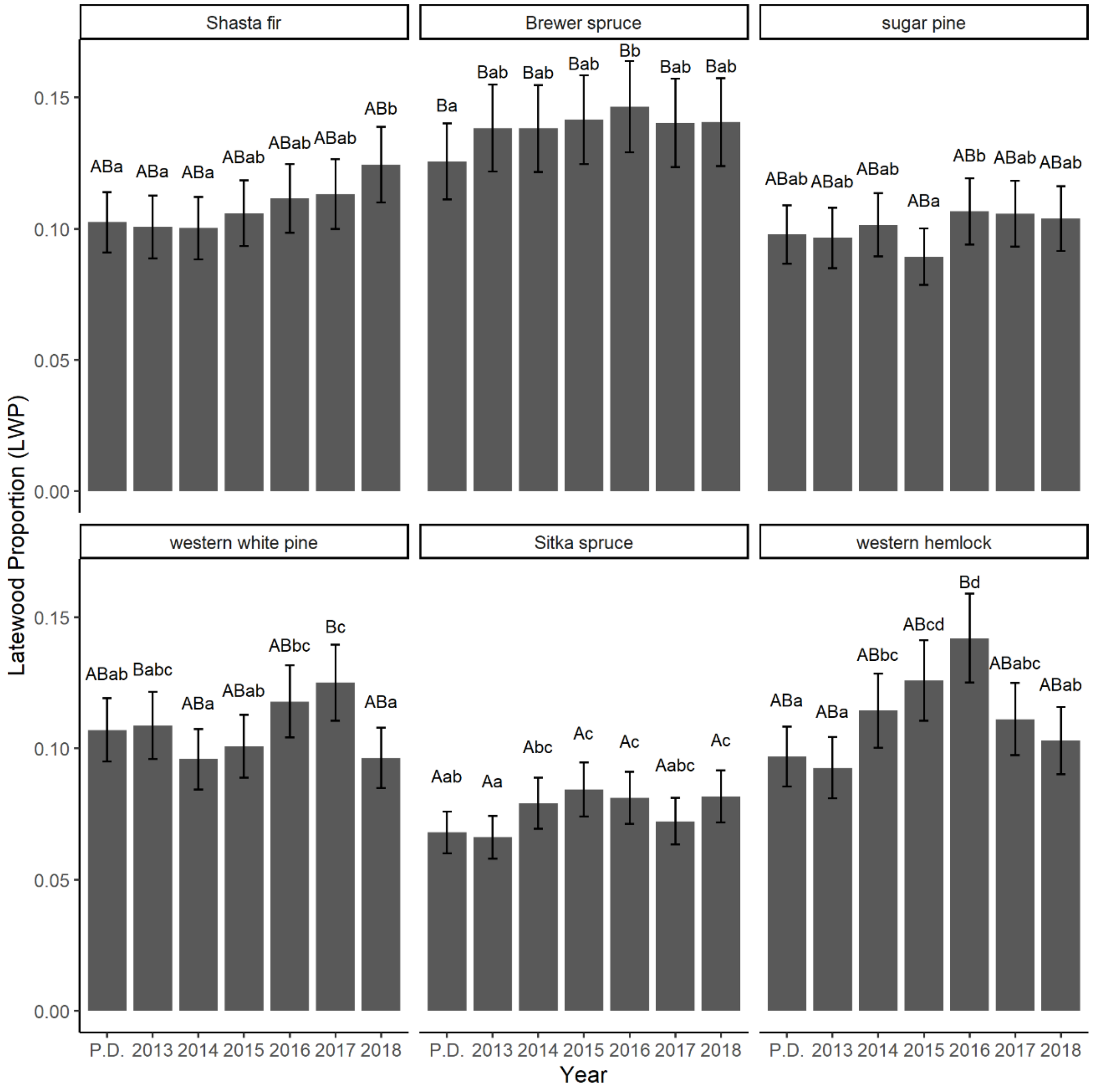

Figure 8. Mean (± SE) annual latewood proportion (LWP) for the averaged pre-drought period (2009-2012) compared to the drought period (2013-2015) and the post-drought period (2016-2018). Within a time period, species not sharing the same uppercase letter are significantly different; within a species, time periods not sharing the same lowercase letter are significantly different.

DISCUSSION

Effects of Competition, Climate, and Site and Tree Characteristics on Growth

The effects of competition, moisture availability (PDSI), and tree size on growth varied among the six conifer species. A recent meta-analysis of stand-level competition dynamics showed that competition does not affect tree growth in a unidirectional way and local-scale interactions may be quite nuanced (Castagneri et al., 2022). Correspondingly, in northern California, the influence of competition on growth varied among conifer species. As expected, competition constrained growth in Shasta fir, Brewer spruce, and sugar pine, likely due to the use of shared limiting resources. Notably, Shasta fir, an endemic hybrid species in northern California, was the only species negatively affected by interspecific competition, likely due to a heightened vulnerability to pests and pathogens compared to other co-occurring species (Desiervo et al., 2018). Additionally, this study's protocol to avoid locations with high mortality (e.g., many sites dominated by Shasta fir, pers. observation) may have biased sampling to sites with minimal Shasta fir representation relative to other species, possibly increasing the effect of interspecific competition on Shasta fir.

Contrastingly, competition (Hegyi index) was not a strongly limiting factor for one montane species (western white pine) or the two coastal species (Sitka spruce and western hemlock). Previous findings show that competition does not always constrain growth or reduce drought tolerance (Castagneri et al., 2022), and can be less important than tree age and size effects (Lebourgeois et al., 2014; Gillerot et al., 2021). Competition is generally expected to have a negative effect on radial growth in some coastal species (i.e., redwood and Douglas-fir) in young, dense stands that have been recently harvested in this region (Soland et al., 2021; Dagley et al., 2018), which contrasts findings from this study of Sitka spruce and western hemlock in unharvested stands. In contrast, in western white pine (montane) and Sitka spruce (coastal), crown ratio had a relatively strong positive effect on growth, and is often negatively correlated with competition and stand density (Garber and Maquire, 2005; Kramer et al., 2018; Owen et al., 2021). However, I found no clear relationship between crown ratio and competition for these two species in this study. Trees per hectare (TPH), a density-driven metric of competition, reduces stomatal regulation in Sitka spruce and western hemlock (Robinson, 2021). This suggests that competition likely influences drought response and growth of coastal species in stand conditions that are denser than the stands sampled in this study.

As expected, PDSI had a positive effect on diameter growth in all species with the exception of sugar pine. Current year PDSI was significant in Sitka spruce, while a 2-year lagged PDSI was significant in Shasta fir, Brewer spruce, western white pine, and western hemlock. Species-level growth responses to moisture availability vary and can have lagged effects (Breda et al., 2006; Hurteau et al., 2007), possibly due to dependence on previous years snow and soil moisture. Although individual species had varied growth responses to drought, almost all were negatively affected by dry years. This negative influence of dry years on growth in coastal species (Sitka spruce and western hemlock) was expected, and likely attributable to limited carbon uptake during drought due to increased stomatal regulation (Robinson, 2021). However, the negative effect of dry years on growth in montane species (Shasta fir, Brewer spruce, and western white pine) is interesting. Stomatal conductance in these three montane species did not appear to increase during drought (Robinson, 2021), so it would be expected that growth would have continued uninhibited. It is likely that minimal stomatal regulation during drought allowed cavitation and loss of hydraulic capacity, which ultimately hampered growth. Like other montane conifer species, sugar pine also exhibited minimal stomatal regulation during drought (Robinson, 2021), although PDSI did not have a significant effect on growth. Thus, the unfettered growth during drought, coupled with continued stomatal conductance under dry conditions, suggests that sugar pine wood anatomy is relatively resistant to cavitation and maintains high levels of hydraulic capacity under drought conditions (McDowell et al., 2008). While this seeming vigor during drought coupled with sugars pine’s occurrence on sites that are already relatively dry (and therefore likely acclimated to dry conditions; Kauffmann, 2012) could indicate that this species should be relatively resistant and resilient to drought, this species is suffering some of the greatest mortality in the region (Lemmo, 2022), likely due to a high vulnerability to pests and pathogens.

Larger, more complex crowns are associated with increased photosynthetic capacity (Kramer et al., 2018; Poudel et al., 2021) and higher foliar water uptake in some conifers (Kerhoulas et al, 2020). Greater ability to intercept precipitation and light may have supported faster diameter growth in individuals with fuller crowns. These relationships support the findings of a positive correlation between crown ratio and diameter growth in four of six species in this study with the exception of sugar pine and western hemlock. For western hemlock, crown ratio may not have been an important determinant of growth due to this species' high shade tolerance. Rather, the positive correlation between growth and DBH measured in western hemlock could be due to greater non-structural carbohydrates (NSC) in larger trees (Sala et al., 2011). Because NSCs act as energy reserves during periods of reduced photosynthesis (Ji et al., 2020), they may have supported radial growth in larger diameter western hemlocks during the entire study period.

Species-level Drought Response

Drought responses varied between coastal and montane species, suggesting differences in physiological strategies to deal with water stress under extreme and prolonged droughts, which is reported among many conifer species (Marques et al., 2016; Salazar-Tortosa et al., 2018; Robinson, 2021). These different strategies result from a combination of site-specific demands and species-specific adaptations to the climatic conditions of their natural ranges (Millar et al., 2007; Brodribb et al., 2014). Coastal species (Sitka spruce and western hemlock) had low resistance followed by increasing resilience. Three of the montane species (Brewer spruce, sugar pine, and western white pine) had high resistance and resilience, with transiently low resilience in western white pine, while Shasta fir had high initial resistance followed by continuously decreasing resilience.

Coastal species

Across successive drought years, coastal species experienced significant decreases in drought resistance followed by increased resilience 1-2 years post-drought. Immediate growth reductions at the onset of drought suggest that Sitka spruce and western hemlock exercise higher stomatal regulation (Robinson, 2021) and are less acclimated to water stress (Orwig and Abrams, 1997) than montane species. While increased stomatal regulation and latewood production can prevent cavitation and embolism during water stress, they can also reduce carbon uptake and ultimately hamper radial growth during prolonged drought (Truillo et al., 2012; Das et al., 2013; Robinson, 2021).

Low drought resistance in coastal species is likely related to temperature, rooting patterns, and fog. Annual average maximum temperatures were higher at coastal sites than montane sites during the study period, and may partially explain the relatively low resistance and increasing LWP measured in coastal species (e.g., Martin-Benito et al., 2013). The root systems of western hemlock are relatively shallow and lack tap roots (Burns and Honkala, 1990), increasing reliance on moisture in upper soil horizons and foliar water from summer fog. The drought period likely reduced upper horizon soil moisture (Pompa-Garcia et al., 2021) and fog inputs (Johnstone and Dawson, 2010), leading to increased water stress in western hemlock. Sitka spruce has relatively fast-growing, complex crowns (Kramer et al., 2018) that maximize photosynthetic capacity (Poudel, 2021), foliar water uptake (Kerhoulas et al. 2020), and growth. However, larger crowns can also can reduce drought resistance (Roberts and Harrington, 2008) via increased transpirational water demands during dry periods (McDowell et al., 2008).

In the final two years of the study period both coastal species increased resilience, with Sitka spruce returning to the 2013 growth rate by 2017 and western hemlock increasing growth in 2017 and 2018. Increasing trends in resilience may indicate that coastal species altered xylem anatomy in response to water stress. Increasing LWP may have helped reduce xylem cavitation and maintained more consistent hydraulic conductivity, allowing resources to be conserved for diameter growth instead of xylem tissue repair once the drought subsided. Cavitation resistance is one of the most important defenses against internal damage caused by water stress and has been directly linked to drought resistance and resilience in several conifer species (Brodribb and Cochard, 2008; Bouche et al., 2014). Many studies show that conifers are capable of acclimating to changes in water stress by adjusting their xylem anatomy (e.g., decreasing cell diameters, increasing cell wall thickness, increasing latewood production) to reduce cavitation risk and prevent water loss at the cost of reduced secondary growth during drought (Fonti and Jansen, 2012; Gazol et al., 2016, Huang et al., 2017 and 2021). However, three years of resilience values below 1 imply that coastal conifers were generally acclimated to wetter conditions, and may not be well adapted to withstand the changes in moisture availability that occurred during the 2013-2015 drought (Zwieniecki and Seechi, 2015; Isaac-Renton et al., 2018; Desoto et al., 2020). Nonetheless, coastal sites had relatively low drought-induced mortality compared to montane sites in the region (Lemmo, 2022), indicating drought tolerance via an alternative metric.

Montane species

All four of the montane species illustrated remarkably high levels of resistance during the drought period followed by varied post-drought resilience and production of latewood. The resistance values agree with previous studies of dry-adapted conifers that exhibit high levels of drought tolerance (Bouche et al., 2014; Gazol et al, 2018), and suggest acclimation to water stress (Orwig and Abrams, 1997). Resistance in these montane species is likely attributable to limited stomatal regulation (Robinson, 2021) that leads to maintaining high levels of photosynthesis, and therefore diameter growth early in the drought. However, post-drought resilience varied; Shasta fir and western white pine showed significant growth reductions, whereas Brewer spruce and sugar pine remained unchanged.

Reduced post-drought resilience in Shasta fir (2016-2018) corroborates evidence of tree mortality during the same time due to a combination of biotic (dwarf mistletoe and beetles) and drought (Mortenson et al., 2015; DeSiervo et al., 2018) stress. Limited stomatal regulation (Robinson, 2022) and LWP (this study) appears to have significantly reduced resilience for at least three years following the drought that may contribute to regional tree mortality (e.g., Desoto et al., 2020).

In contrast, Brewer spruce and sugar pine maintained generally consistent growth rates throughout the study period (i.e., high drought resistance and resilience). Growth-based resistance and resilience in Brewer spruce was notably high, whereas LWP was significantly higher in 2016 compared to the pre-drought period. This increase in latewood production likely helped maintain hydraulic conductivity, prevent embolism, and support continued growth following water stress. Brewer spruce prefers north- or east-facing slopes and is generally of co-dominant or intermediate canopy class in mixed-species stands (Kauffmann, 2012). Thus, the limited exposure to solar radiation provided by cover from canopy-dominant neighboring species and preferential aspect may create microclimates that minimize evapotranspiration and soil drying (Ma et al., 2010; Arx et al., 2013) during drought. Standardized drought indices may not capture small-scale variations in moisture availability (Schwarz et al., 2020) that potentially allow for higher levels of growth at specific locations despite the regional drought conditions measured at the site level. Finally, Brewer spruce is a paleo-endemic species in the Klamath Mountains that has weathered long-term climate changes since the Cenozoic period (Kauffmann, 2012). As such, it has a highly limited geographic range, but is well-adapted to its current range, even in the face of drought stress.

The high drought resistance and resilience measured in sugar pine does not align with prior findings of recent mortality (Byer and Jin, 2017; DeSiervo et al., 2018; USDA, 2021), as tree death is generally preceded by reduced diameter growth and declining resilience (Das et al., 2007; Calleret et al., 2017; Desoto et al., 2020). Tree mortality of sugar pine at the same sites was common, but more than 90% of the death dates recorded occurred prior to the drought (Lemmo, 2022). This suggests contribution of factors such as white pine blister rust and insect attack (Schwandt et al., 2013; Das et al., 2016) lead to sugar pine mortality more so than drought alone. Both short- (< 10 years) and long-term (10-40 years) growth variability have proven to be informative predictors of conifer mortality (Bigler and Bugman 2003; Das et al., 2007; Kane and Kolb, 2014; Slack et al., 2021). In this study, drought resistance and resilience of sugar pine was measured over a relatively short study period (2013-2018), and did not evaluate long-term growth declines that may contribute to more broad-scale mortality. On the other hand, the relatively high resistance and resilience values that counter trends in conifer mortality may also highlight a weakness of drought response metrics. Measures of resistance and resilience calculated following Lloret et al. (2011) are highly dependent on the selection of pre-drought, drought, and post-drought periods (Schwarz et al., 2020). Although the annual average PDSI of the selected pre-drought period was not water-limited (PDSI > 0), tree growth is determined by multiple factors. Additionally, microsite and sub-annual differences in timing and intensity of drought conditions may have varied to some degree across sampling locations (Zang et al., 2019).

Western white pine’s wide ecological amplitude allows it to tolerate a large degree of site and environmental variation. Despite two years of reduced resilience in western white pine, the increase that followed in 2018 was the largest measured across all species. Additionally, LWP was relatively unchanged during the drought period followed by a significant post-drought increase in 2017. Mature western white pine are often taller and more deeply rooted than conspecifics (Harvey et al., 2008), affording them greater access to light and deep soil water reserves. While limited stomatal control (Robinson, 2021) appears have reduced diameter growth following the drought period (presumably due to reduced hydraulic capacity from cavitation during drought), better access to light and soil moisture may have fueled eventual increases in resilience. Drought tolerance in conifers from more arid environments can also be related to intraspecific phenotypic plasticity (Ziaco et al., 2014) in which individuals adjust their anatomy or phenology to cope with environmental stressors like drought. A recent study of western white pine genetic variation found that populations in northern California and southern Oregon hold the majority of intraspecific genetic variation found within the entire species (Kim et al., 2011). This suggests that harsh or prolonged drought conditions may contribute to local adaptations (i.e., increasing drought tolerance; Depardieu et al., 2020).

Conclusions and Management Implications

Radial growth in both of the two coastal and four montane conifer species was influenced by tree size (DBH) or crown ratio as well as moisture availability (PDSI). However, competition only influenced growth in montane species. Interestingly, all six species endured the recent drought in northern California with reasonably high initial resistance, but as the 2013-2015 drought proceeded, coastal species showed marked reductions in drought resistance and resilience (2016-2018) and increased latewood proportion. The lower resistance observed in coastal species suggests that they may be at risk of reduced growth during more severe, prolonged, and/or frequent droughts. However, increasing trends in post-drought resilience indicate they may be able to recover from stressors similar to the 2013-2015 drought. On the other hand, while resistance and resilience of montane species (Brewer spruce, western white pine, and sugar pine) were reasonably high, pine mortality persists in the region, suggesting pests and pathogens are the main drivers of decline. Likewise, reduced resilience and delayed increases of LWP in Shasta fir suggest that growth decline and mortality are likely to continue for this regionally endemic hybrid. These study sites represented relatively dense, mixed-conifer stands in northern California (i.e., lack of wildfire) with a specific range of competition values for each species, which should be recognized when extending these results to other forest types or broader scales.

Growth reductions caused by drought stress were varied across the six conifer species studied in northern California. Thinning and/or prescribed fire may mitigate negative effects of drought and promote radial growth in northern California forests (e.g., Sohn et al., 2016, Lalemand, 2018, Vernon et al., 2018). On the coast, such treatments could be a feasible means to improve drought resilience in non-old growth Sitka spruce and western hemlock trees such as the ones sampled in this study. Crown ratio (Sitka spruce) and DBH (western hemlock) had the highest positive influence on diameter growth at coastal sites and would likely increase in response to mechanical thinning treatments (Soland et al. 2021). In montane environments, prescribed fire may also reduce stand density, which in turn may help prevent the spread of pests and pathogens that reduce resilience in Shasta fir (Desiervo, et al., 2018) and decrease mortality of western white pine and sugar pine (Martinez-Vialata., 2004; van Mantgem et al., 2004; Lemmo, 2021). Drought, pests, pathogens, and altered fire regimes interact to likely form a stress complex (Franklin et al., 1987; Das et al., 2016), which may continue to threaten the diversity and vigor of northern California’s coastal and montane mixed-conifer forests. Further exploration of diverse forest species’ response to multiple drought periods, and interactions with biotic stressors and fire, would further inform management and conservation efforts.

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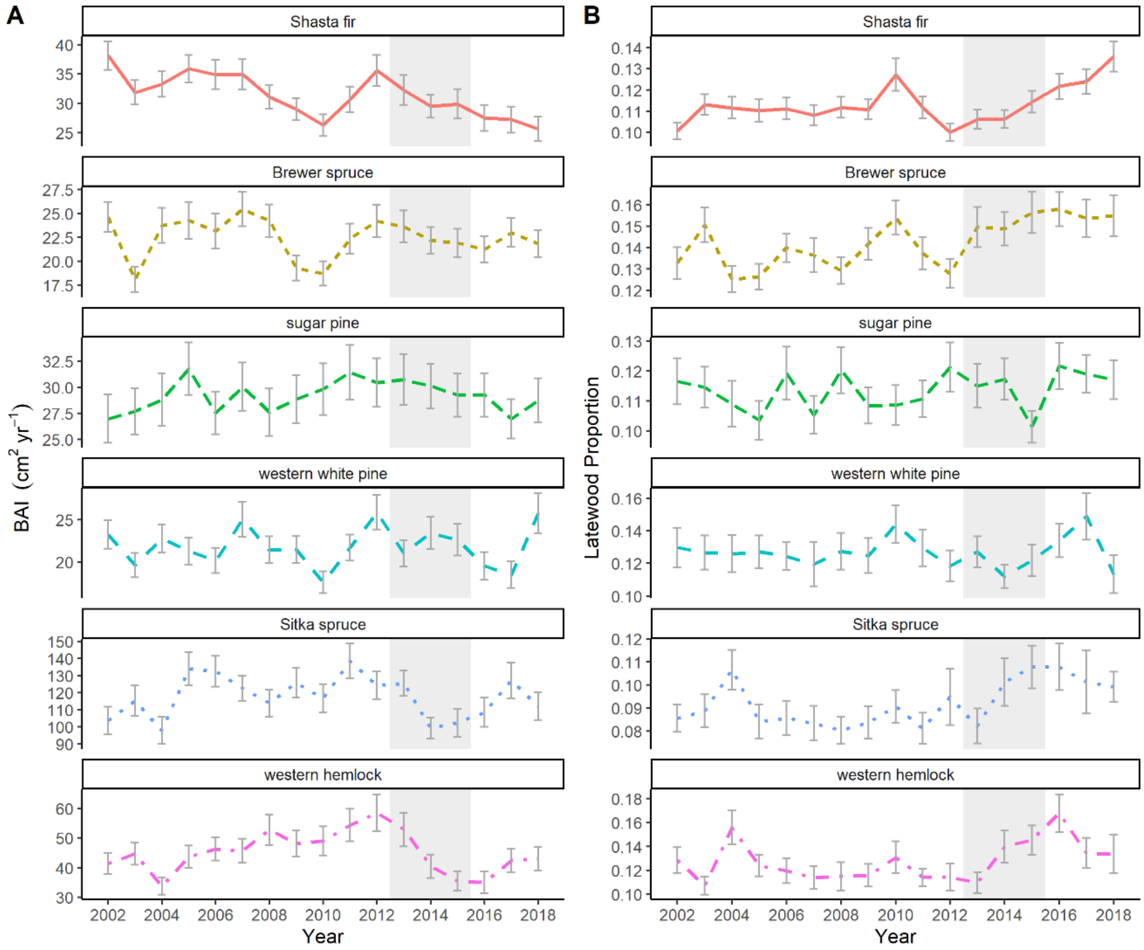
APPENDICES

Appendix A. Mean (± SE) BAI (A) and LWP (B) for each species across the entire study period (2002-2018).



Appendix B. All potential predictor variables that were evaluated for use in growth models.

Predictor	Description
Palmer Drought Severity Index (PDSI)	Standardized index of moisture availability. Values less than 0 indicate water-stress that is higher than the long-term average.
Lagged Palmer Drought Severity Index (PDSI Lag)	Moisture availability lagged by 1, 2, and 3 years. Some conifers may have lagged growth responses to water-stress.
Annual Precipitation (PPT)	Annual average precipitation (mm). Reductions in annual precipitation may lead to reduced radial growth.
Water-Year Precipitation (PPT WY)	Annual average precipitation (mm) from the previous year's October through the current year’s September.
Total Competition (CI Total)	Total neighborhood competition (Hegyi). Competition for shared resources may affect radial growth.
Interspecific Competition (CI Inter)	Neighborhood competition (Hegyi) from contraspecifics.
Intraspecific Competition (CI Intra)	Neighborhood competition (Hegyi) from conspecifics. Intraspecific competition may have a stronger effect due to use of the same suite of resources.
Diameter at Breast Height (DBH)	Tree diameter (cm) at 1.37 m height. Larger trees may have greater energy reserves or deeper roots that can access different water sources.
Crown Ratio (CR)	Percentage of live crown relative to total tree height. Trees with larger crowns may have greater photosynthetic capacity or higher transpirational demand.
Canopy Position (CP)	Categorized as dominant, co-dominant, or intermediate. Trees in more dominant positions in the canopy may have differential access to light.
Canopy Competition (CC)	Categorized as 1-4 based on amount surrounding canopy trees direct overlap of the focal tree’s crown.
Minimum Temperature (Tmin)	Minimum annual average temperature (°C). Higher values indicate warmer winters which could lengthen the growing season.
Maximum Temperature (Tmax)	Maximum annual average temperature (°C). Higher values indicate warmer summers which could increase evapotranspiration during dry periods.

Predictor	Description
Heat Load Index (HLI)	Standardized index of direct solar radiation at the site level. Higher values indicate greater light availability and higher potential evapotranspiration.
Snow Water Equivalent (SWE)	Estimate of liquid water contained in snowpack (mm). Lower moisture inputs from reduced snow pack could reduce radial growth at montane sites.
30-Year Average Precipitation (PPT 30)	Average annual precipitation from 1981-2010 (mm). Higher values correspond with greater long-term site-level moisture availability.

Appendix C. Top linear mixed effects models for all conifer species and for pooled coastal species. Predictor variables include: Interspecific competition (CI Inter), intraspecific competition (CI Intra), total competition (CI Total), crown ratio (CR), PDSI, 2-year lagged PDSI (PDSI Lag2), diameter at breast height (DBH), canopy position (CP), canopy competition (CC), and minimum annual temperature (Tmin). Best models are bolded.

Species	Predictors	df	logLik	AIC	ΔAIC
Shasta fir	**CI Inter, CR, PDSI Lag2**	**11**	**-11840.8**	**23703.6**	**0.0**
	CI Inter, CR, DBH, PDSI Lag2	12	-11839.9	23703.8	0.2
	CI Inter, CR, CP, PDSI Lag2	12	-11840.2	23704.4	0.8
	CI Inter, CR, CP, DBH, PDSI Lag2	13	-11839.6	23705.1	1.5
	CI Inter, PDSI Lag2	10	-11843.2	23706.3	2.7
	CI Inter, DBH, PDSI Lag2	11	-11842.4	23706.8	3.2
	CI Inter, CP, PDSI Lag2	11	-11842.5	23707.1	3.5
	CI Inter, DBH, CP, PDSI Lag2	12	-11842.1	23708.1	4.5
	CR, DBH, PDSI Lag2	11	-11843.5	23708.9	5.3
	CR, DBH, CP, PDSI Lag2	12	-11842.8	23709.7	6.1
	CR, CP, PDSI Lag2	11	-11844.4	23710.7	7.1
	CI Inter, CR, Tmin	11	-11844.4	23710.8	7.2
	CI Inter, CR, DBH, Tmin	12	-11843.6	23711.3	7.7
	CI Inter, CP, Tmin	12	-11843.7	23711.5	7.9
	CR, PDSI Lag2	10	-11845.8	23711.6	8.1
	DBH, PDSI Lag2	10	-11845.8	23711.7	8.1
	DBH, CP, PDSI Lag2	11	-11845.2	23712.3	8.7
	CI Inter, CR, DBH, Tmin, CP	13	-11843.2	23712.5	8.9
	CP, PDSI Lag2	10	-11846.4	23712.9	9.3
	CI Inter, Tmin	10	-11846.7	23713.3	9.8
Brewer spruce	CR, CI Total, CC, PDSI Lag2	12	-11360.3	22744.7	0.0
	CR, CI Total, PDSI Lag2	**11**	**-11361.6**	**22745.1**	**0.4**
	CR, CC, PDSI Lag2	11	-11361.8	22745.6	0.9
	CR, CI Total, Tmin, CC	12	-11362.0	22748.0	3.3
	CR, CI Total, Tmin	11	-11363.2	22748.4	3.7
	CR, PDSI Lag2	10	-11364.3	22748.6	4.0
	CR, Tmin, CC	11	-11363.5	22749.1	4.4
	CI Total, CC, PDSI Lag2	11	-11365.1	22752.1	7.4
	CR, Tmin	10	-11366.2	22752.3	7.6
	CI Total, PDSI Lag2	10	-11366.6	22753.1	8.5

Species	Predictors	df	logLik	AIC	ΔAIC
	CI Total, CC, Tmin	11	-11366.3	22754.7	10.0
Western white pine	CR, CI Inter, PDSI Lag2	11	-9919.5	19861.0	0.0
	CR, CI Inter, DBH, PDSI Lag2	12	-9918.6	19861.2	0.2
	CR, DBH, PDSI Lag2	11	-9919.9	19861.8	0.8
	CR, PDSI Lag2	**10**	**-9921.3**	**19862.6**	**1.6**
	CI Inter, PDSI Lag2	10	-9923.5	19867.0	5.9
	CI Inter, DBH	11	-9923.0	19868.0	7.0
Sugar Pine	**CI Total**	**9**	**-11332.9**	**22683.9**	**0.0**
	CI Total, Tmin	10	-11332.0	22684.0	0.1
	CI Total, DBH	10	-11332.3	22684.7	0.8
	CI Total, DBH, Tmin	11	-11331.4	22684.8	1.0
	CI Total, PDSI	10	-11332.6	22685.2	1.4
	DBH	9	-11333.8	22685.6	1.8
	DBH, Tmin	10	-11332.9	22685.8	2.0
	CI Total, DBH, PDSI	11	-11332.0	22686.0	2.2
	DBH, PDSI	10	-11333.5	22687.0	3.2
	Intercept Only	8	-11335.9	22687.7	3.9
	Tmin	9	-11334.9	22687.9	4.0
	PDSI	9	-11335.6	22689.1	5.3
Sitka spruce	CR, DBH, PDSI	11	-13576.2	27174.5	0.0
	CR, PDSI	**10**	**-13577.8**	**27175.5**	**1.0**
	CR, DBH, CC	12	-13576.1	27176.1	1.7
	CC, PDSI	10	-13578.1	27176.3	1.8
	CR, DBH, PDSI, CI Intra	12	-13576.2	27176.3	1.8
	DBH, PDSI, CC	11	-13577.2	27176.4	1.9
	DBH, PDSI	10	-13578.2	27176.4	1.9
	CR, PDSI, CC	11	-13577.2	27176.5	2.0
	CR, PDSI, CI Intra	11	-13577.3	27176.6	2.2
	PDSI	9	-13579.8	27177.7	3.2
	CR, PDSI, CI Intra, CC	12	-13577.0	27178.1	3.6
	PDSI, CI Intra, CC	11	-13578.0	27178.1	3.6
	CR, DBH, PDSI, CI Intra, CC	13	-13576.0	27178.1	3.6
	DBH, PDSI, CI Intra	11	-13578.1	27178.2	3.7
	DBH, PDSI, CI Intra, CC	12	-13577.2	27178.4	3.9
Western Hemlock	DBH, PDSI Lag2, CP	11	-11200.5	22423.0	0.0
	DBH, PDSI Lag2	**10**	**-11202.3**	**22424.7**	**1.7**
	DBH, CI Inter, PDSI Lag2, CP	12	-11200.4	22424.9	1.9
	DBH, CI Inter, PDSI Lag2	11	-11202.0	22426.0	3.0

Species	Predictors	df	logLik	AIC	ΔAIC
	DBH, CP	10	-11205.3	22430.6	7.6
	CI Inter, PDSI Lag2, CP	11	-11204.6	22431.1	8.1
	PDSI Lag2, CP	10	-11206.0	22432.0	9.0
	DBH	9	-11207.1	22432.2	9.2
	DBH, CI Inter, CP	11	-11205.2	22432.4	9.4
Coastal Pooled	**DBH, Crown Ratio, PDSI**	**9**	**-24844.0**	**49706.0**	**0.0**
	DBH, Crown Ratio, CI Inter, PDSI	10	-24843.5	49706.9	0.9
	DBH, Crown Ratio, PDSI, CP	10	-24843.9	49707.7	1.7
	DBH, Crown Ratio, PDSI, CI Inter, CP	11	-24843.4	49708.8	2.9
	DBH, PDSI, CC	9	-24845.5	49709.0	3.0
	DBH, CI Inter, PDSI, CC	10	-24845.2	49710.5	4.5
	DBH, PDSI	8	-24847.6	49711.2	5.3
	DBH, CI Inter PDSI	9	-24846.9	49711.8	5.8