



RESEARCH ARTICLE

Low stand density moderates growth declines during hot droughts in semi-arid forests

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Abstract

1. Increasing heat and aridity in coming decades is expected to negatively impact tree growth and threaten forest sustainability in dry areas. Maintaining low stand density has the potential to mitigate the negative effects of increasingly severe droughts by minimizing competitive intensity.
2. However, the direct impact of stand density on the growing environment (i.e. soil moisture), and the specific drought metrics that best quantify that environment, are not well explored for any forest ecosystem. We examined the relationship of varying stand density (i.e. basal area) on soil moisture and stand-level growth in a long-term (multi-decadal), ponderosa pine *Pinus ponderosa*, forest management experiment. We accounted for the influence of stand-level density on moisture availability by measuring and modelling soil moisture using an ecosystem water balance model.
3. To quantify the growing environment, we developed metrics of ecological drought that integrate the influence of moisture availability in the soil with moisture demand by the atmosphere. We paired these results with stand-level dendrochronological data, avoiding the potential bias introduced from individual tree-based assessments, and used critical climate period analysis to identify the timing and duration of these drought metrics that most relate to forest growth.
4. We found that stand-level growth is highly responsive to the combination of high temperature and low soil moisture. Growth in all stands was negatively related to temperature and positively related to moisture availability, although the sensitivity of growth to those conditions varied among stand density treatments. Growth enhancement during cool years is greatest in low density stands. In addition, low density stands displayed substantially higher long-term average growth than higher density stands and maintained higher growth even when temperatures were high. Growth in low density stands also increased more than higher density stands in response to greater long-term moisture availability.
5. *Synthesis and applications.* We quantified the influence of stand-level density on the environmental conditions that determine tree growth and related forest growth to patterns of moisture supply and demand. Our drought metrics, and

analytical approach for quantifying drought impacts on forest growth, are a novel approach for assessing forest vulnerability to drought under climate change. These results provide new perspective on the potential for density management to mitigate drought stress and maintain forest stand growth during and after drought events in water-limited forests.

KEYWORDS

climate adaptation, dendrochronology, drought stress, ecological drought, forest management, soil moisture, stand density, stand growth

1 | INTRODUCTION

Climate models agree that with rising temperatures in the 21st century, many dryland regions will experience an increase in the frequency, severity and duration of droughts, leading to overall lower soil moisture, increased plant drought stress, heightened susceptibility to insect and disease outbreaks (Kolb et al., 2016), and amplified wildfire risk (Ziegler, Hoffman, Battaglia, & Mell, 2017). Already, hot drought conditions, defined as below-average precipitation and markedly increased evaporative demand due to higher temperatures (Udall & Overpeck, 2017), have been observed globally, and particularly in the southwestern United States (Williams et al., 2013). These droughts have demonstrated impacts on forests that are expected to increase in coming decades, including impeded regeneration (Petrie et al., 2017), reduced growth (Berdanier & Clark, 2016; Bottero et al., 2017), and increased tree mortality (Bradford & Bell, 2017; Williams et al., 2013). At the landscape level, these impacts may promote dramatic shifts in forest communities (Clark et al., 2016) with potential transitions to non-forested ecosystems, generating cascading impacts on key ecosystem services, including carbon sequestration, hydrologic regulation and recreation. Quantifying the particular drought conditions that most influence forests may guide forest adaptation strategies as droughts become more frequent and severe.

Reducing stand density (i.e. tree basal-area [BA] per ha) is one approach to mitigate the negative effects of increasingly severe droughts due to climate change (Bottero et al., 2017; Bradford & Bell, 2017; D'Amato, Bradford, Fraver, & Palik, 2013; Gleason et al., 2017; Sohn, Saha, & Bauhus, 2016). Forest sensitivity to drought is determined by a number of factors, including tree species composition (Teets, Fraver, Weiskittel, & Hollinger, 2018), hydraulic traits (Bréda, Huc, Granier, & Dreyer, 2006), local genotypic variation, soils and stand density (D'Amato, Bradford, Fraver, & Palik, 2011). Stand density is unique amongst these factors because it can be directly manipulated, often with co-benefits, including reduced forest fire severity. Furthermore, stand density is often used as a proxy for competition intensity, which influences regeneration, growth and mortality rates in all forests (Hille Ris Lambers, Clark, & Beckage, 2002). Although reducing density has been shown to decrease competition for scarce water resources during droughts, how soil moisture varies in response to stand density, and how these differences

interact with atmospheric moisture demand to effect forest growth and drought resistance, remain unclear. Untangling the interacting effects of stand density, moisture availability in the soil and temperature-driven moisture demand by the atmosphere is critical to anticipate forest growth under various density and future climate scenarios (Clark et al., 2016).

Climate conditions and soil moisture are recognized as the primary drivers of inter-annual forest growth variability, reflecting energy and water demands for photosynthesis and carbon assimilation (Toledo et al., 2011). Numerous dendrochronological studies have linked decreasing annual tree-level radial growth to drought (Berdanier & Clark, 2016; Truettner et al., 2018); however, tree-level response to drought does not directly scale up to stand-level response due to within stand spatial heterogeneity of structure and growth environments (Foster, Finley, D'Amato, Bradford, & Banerjee, 2016). Furthermore, individual tree dendrochronology assessments have the potential to introduce bias if trees are selected for their potential sensitivity to climate-growth relationship (Carrer, 2011; Nehrbass-Ahles et al., 2014). Focus has recently shifted towards stand-level assessments of growth, in order to evaluate whole stand response to climate, including resistance and resilience to drought (D'Amato et al., 2013; Gleason et al., 2017; Teets et al., 2018). Considering stand-level dynamics is particularly important given that most management prescriptions are applied to forest stands, not to individual trees, and stand-level inference requires stand-level assessment (Clark et al., 2016).

It is well understood that drought reduces tree growth, but the specific characteristics of drought that most influence growth are not clear. The timing and severity of drought are both difficult to define, largely because drought definition varies by region (Slette et al., 2019). Although numerous meteorological drought severity indices are available to characterize water deficits (e.g. Palmer Drought Severity Index [PDSI], Standardized Precipitation-Evapotranspiration Index [SPEI], etc.), these metrics are not intended to represent ecological impacts (i.e. ecological droughts; Crausbay et al., 2017). In particular, quantifying ecological droughts requires representing not only meteorological conditions, but also incorporating the influence of vegetation and soil properties on patterns of soil moisture that directly influence plant growth and survival. Soil moisture dynamics are influenced by interactions between seasonal temperature and precipitation

patterns, as well as soil type and vegetation structure, and previous work has demonstrated strong links among seasonality of drought and wetness and inter-annual growth variability in arid forests (Truettner et al., 2018; Williams et al., 2013). However, these studies have not evaluated the influence of drought duration or of lagged conditions that occurred more than 1 year prior to current growing season on stand-level growth, nor have they examined how density influences difference in moisture availability and demand. Projecting the overall impact of future enhanced drought, and accurately assessing the potential benefits of reducing stand density, requires understanding how density itself influences soil moisture and determining when soil moisture most influences stand growth.

Dry forests of the southwestern USA may be particularly vulnerable to drought. Drought has already been observed in this region for much of the last three decades (Williams et al., 2013) and is expected to become more intense in the coming century (Cook, Ault, & Smerdon, 2015). In semi-arid ponderosa pine *Pinus ponderosa* ecosystems in this region, soil moisture availability is frequently limited, and competition for this resource is acute. Anthropogenic modifications to ponderosa pine forest structure, notably increased stand density as a result of 20th century fire suppression (Sackett & Haas, 1998), have further amplified drought stress in this ecosystem (Feeney, Kolb, Covington, & Wagner, 1998). Developing climate adaptation strategies for these vulnerable forests requires understanding how stand density and drought interact to influence patterns of soil moisture and determine overall impacts on forest growth.

Our goal was to understand how stand density alters the severity of soil moisture deficits, and how this in-turn influences stand-level growth response to drought. We examined annually resolved, stand-level growth patterns from stands maintained at a range of densities in a long-term (1962–present) ponderosa pine forest management experiment located in northern Arizona, USA. These detailed data allowed us to address the following objectives. First, we applied an ecosystem water balance model to estimate the effects of stand density on patterns of soil moisture. We hypothesized that soil moisture deficits will differ across densities, with longer and pronounced dry periods in the high density stands. Second, we characterized how the growing environment varies among density treatments by developing and quantifying ecological drought metrics that represent important differences between moisture availability in the soil and moisture demand by the atmosphere, which is primarily driven by temperature. Focusing on these metrics, we identified the seasonal timing and duration of ecological droughts that most relate to forest growth. We hypothesized that growth will be tightly linked to drought metrics that integrate soil moisture and temperature. Third, using equations developed from objective two, we assessed the vulnerability of growth response to each ecological drought and temperature variable across a range of stand density treatments. We hypothesized that growth in higher density stands will be more impacted by the ecological drought metrics. Our results will be essential for accurately anticipating the impact of climate change on dry forest growth and for developing adaptive management strategies.

2 | MATERIALS AND METHODS

2.1 | Site description

This work was conducted in the Taylor Woods study at the Fort Valley Experimental Forest, located in Northern Arizona, USA (35.275, -111.721). The 14.5 ha study site is composed of 100% ponderosa pine that naturally regenerated in 1919, with a grass and shrub understory, primarily composed of Arizona fescue *Fescue arizonica* and blue grama *Bouteloua gracilis*. Climate is defined by moderate temperatures (mean annual temperature = 6.0°C) and is dry (mean annual precipitation = 55.4 cm) with precipitation received bimodally during winter (December–March, 39%) and late-summer, during the monsoon (July–September, 37%). The region regularly experiences drought during May and June. Soils are productive for the region and are classified as relatively deep, well-drained Typic Argiboroll soils derived from volcanic material, primarily basalt (Bailey, 2008; Ronco, Edminster, & Trujillo, 1985). Taylor Woods was established in 1962 and is composed of seven distinct density treatments (5, 9, 14, 18, 23, 28 and 34 m²/ha BA), as well as an untreated control (51 m²/ha) and clear-cut treatment, that have been maintained at target densities on an approximate decadal basis (1962, 1967, 1972, 1982, 1992, 2002 and 2017). Each treatment is replicated in three plots, ranging from 0.3 to 0.5 ha in size. Spacing between plots vary due to stocking levels at the time of treatment implementation, and some plots share a common boundary. Plots with a common boundary were assigned similar treatments to lessen edge effects, while a 20.1 m wide buffer zone, consisting of the same density as the nearby plot, was established around all other plots (Ronco et al., 1985).

2.2 | Growth data

Tree increment cores were extracted at breast height (1.37 m) in 2012 from every tree >10 cm diameter within three randomly placed subplots (11.3 m radius) in four of the treatments: a low (9 m²/ha), medium (23 m²/ha), high (34 m²/ha) and an untreated control. Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating was conducted using the marker year method of Yamaguchi (1991), with verification by COFECHA software (Grissino-Mayer, 2001). These dendrochronology records extend from 1930 to 2011.

We quantified forest growth as annual BA increment (m² ha⁻¹ year⁻¹, BAI). First, we estimated diameter (DBH) inside bark using empirical equations to remove the bark thickness from the field-measured DBH (Keyser & Dixon, 2008). Ring-width series were then adjusted to account for off-centre piths following methods and justification presented in Frelich (2002). Using back reconstruction starting from inside the bark towards the pith, annual individual tree diameter was calculated for the entire ring-width series. Predicted bark thickness was then added back to each annual measurement (Myers, 1963). Individual tree BAs were then calculated from annual

diameter values and summed in a plot to obtain stand-level BA. Finally, the difference in inter-annual values were calculated at the stand level to generate BAI.

Because stand-level BAI values were developed from cores of living trees only, they do not account for tree mortality or the trees that were harvested from treatment plots to maintain the target density throughout the experimental period. To account for this, a correction was applied to the BA values derived from ring widths based on the proportion of BA removed in each harvest event, which was derived from inventory data provided by USFS. This ratio was estimated for each harvest event, and cumulatively applied to current annual stand-level growth values for all prior years. To validate our reconstructed series, stand-level BA was calculated from the historical inventory data and compared for accuracy.

2.3 | Effects of stand density on soil moisture (objective 1)

To assess the effects of stand density on soil moisture we used SOILWAT2 (Schlaepfer & Murphy, 2018), a daily time-step, multiple soil layer, process-based, simulation model of ecosystem water balance that has been validated in several dryland ecosystems (Bradford, Schlaepfer, & Lauenroth, 2014). More information pertaining to the mathematical description of SOILWAT2, as well as the parameterization and validation of our soil moisture simulations, including soil and vegetation characterization, can be found in Appendix S1 in the Supporting Information. After confirming that SOILWAT2 appropriately represents seasonal soil moisture dynamics within these forest stands we simulated daily soil moisture for the entire study period in all stands. We quantified bi-weekly average soil water availability (SWA, cm) as the amount of moisture that could be removed from the soil before reaching a tension of -3.9 MPa (Sperry & Hacke, 2002). Differences in soil moisture among density treatments were evaluated by calculating the z-scores among treatments at different times of the year (biweekly) and depths.

2.4 | Ecological drought drivers of forest growth (objective 2)

We developed two new ecological drought metrics that integrate soil moisture and climate-related growth limitations: relative moisture availability and hot-dry stress, and utilized a previously developed ecological drought metric: wet degree days (WDD; Bradford et al., 2017). While uniform measurements of soil moisture availability have been proposed before (i.e. Vicca et al., 2012), our metrics go further by integrating atmospheric and temperature effects alongside soil moisture availability. To our knowledge, the ecological drought metrics of relative moisture availability and hot-dry stress have not been previously published. *Relative moisture availability* was calculated as SWA divided by potential evapotranspiration (PET, cm). PET was calculated using Penman's (1948) equation (Marvel,

Beyrouly, & Gbur, 1992; Penman, 1948), with adjustments based upon Allen, Pereira, Raes, and Smith (1998) and Sellers (1964). This metric not only accounts for periods of water abundance, but also stress due to high atmospheric demand for water. Similar to other derived moisture indices, where mean annual precipitation is used in lieu of soil moisture (Schenk & Jackson, 2002), the greater the disparity between (low) moisture and (high) PET, the higher the stress and greater chance of experiencing a water-stress-induced cavitation. *Wet degree days* were calculated as the sum of the temperature difference between daily mean temperature and 0°C when mean temperature is greater than 0°C and any soil layer is wet (>-1.5 MPa). *Hot-dry stress* was calculated as the sum of the temperature difference between daily maximum temperature and 28°C when the maximum temperature is greater than 28°C and all soil layers are dry (≤-2.2 MPa). Similar to the concept of growing degree days, the latter two metrics directly account for temperature, but with hot-dry stress only accumulating on days with conditions considered to negatively impact growth. The specific criteria used to calculate all three metrics are defined in Table 1 (Stress and Wetness Metrics).

We used a correlation approach referred to as critical climate period analysis (CCP) to identify the best relationships between the timing and duration of the ecological drought metrics introduced above and forest growth across density treatments (Craine et al., 2012). This approach does not rely on any a priori expectations of when drought stress is important; instead periods with the highest correlation are selected for further analysis. A more in-depth description of CCP is provided in Appendix S2.

The ecological drought periods selected, as well as a number of climate-only measures (Table 1) and annual stand density (BA, $\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$), were then entered into a stepwise linear regression model to determine a growth equation. While stepwise regression can inadvertently drop casual variables, we sought to create a parsimonious equation with a few significant climate predictors that can be applied to various density and climate scenarios.

2.5 | Influence of stand density on growth response to ecological drought (objective 3)

The impact of stand density on growth response to ecological drought was examined by predicting growth across a range of densities (10, 15, 20, 30, 40, 50 m^2/ha) using the growth equation established in objective 2. These densities represent BAs commonly found in dry forests of the southwest. Predictions were made by allowing one independent variable to vary at a time, while holding all others at respective constants (the mean of observed values), in order to illustrate the impact of individual ecological drought and climate effects at different densities. These relationships were visualized with proportional growth (BAI/BA) on the y-axis. Proportional growth accounts for annual wood accrual in a treatment relative to the treatment BA for that year and is a better evaluation of comparative stand-level growth across multiple densities than is absolute BAI. Sensitivity to both temperature and the ecological drought

TABLE 1 Climate and ecological drought variables considered for growth analysis across various stand densities

Variable	Definition	Relationship to growth
Climate variables		
AnnualSumPPT	Annual sum of precipitation (cm)	+
AnnualMeanTemp	Annual mean temperature (°C)	+
AnnualMinTemp	Annual daily minimum temperature in the coldest month (°C)	+
AnnualMaxTemp	Annual daily maximum temperature in the hottest month (°C)	-
TemperatureDiff	Difference between AnnualMaxTemp and AnnualMinTemp	-
FrostFreePeriod	Number of consecutive days when minimum temperature is above 0°C	-
Ecological drought metrics		
Moisture availability ratio	Sum of available soil water (cm) in all layers (at a critical threshold of -3.9 MPa) divided by potential evapotranspiration (cm)	+
Hot-dry stress	Sum of the temperature difference between the daily max temperature and 28°C when maximum temperature is >28°C and ALL soil layers are dry (≤ -2.2 MPa)	-
Wet degree days	Sum of the temperature difference between the daily mean temperature and 0°C when mean temperature is >0°C and ANY soil layer is wet (> -1.5 MPa)	+
Stand variables		
Basal area	Annual treatment level basal area (m^2/ha)	+

metrics were then evaluated by inspecting the slope of these fitted relationships.

All analyses were performed in R (R Core Team, 2019).

3 | RESULTS

Periodic thinning in these stands successfully maintained the desired gradients of stand densities (Figure 1). The treatments consistently differed in BA, BAI (highest in stands with high BA) and proportional growth (highest in stands with low BA after 1973)

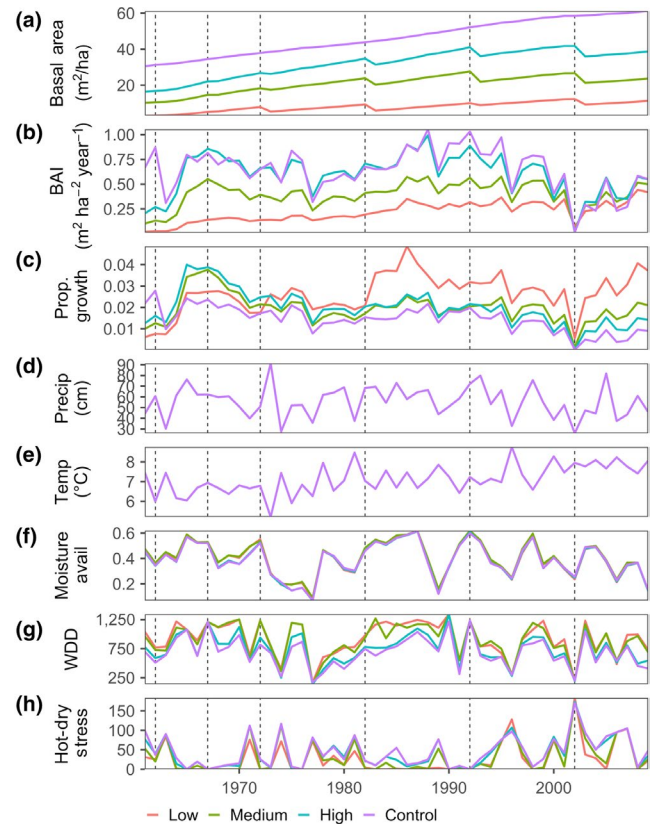


FIGURE 1 Long-term time series (1960–2010) of basal area (m^2/ha , a), basal area increment (BAI; $\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$, b), proportional growth (BAI/BA, c), weather (precipitation and temperature, d & e), and drought stress metrics (f–h, *described in the text) at Fort Valley Experimental Forest. WDD is the abbreviation for wet degree days. Dashed lines indicate years where plots were thinned to implement or maintain treatment density. The four basal area treatments (low, medium, high and control) refer to ponderosa pine stands with basal area of 9, 23 and $34 \text{ m}^2/\text{ha}$, and an untreated control plot

throughout the study period (Table 2). The standard deviation of BAI over the entire study period was greatest in high density stands, while the coefficient of variation was highest at the lowest densities. By contrast, variation in proportional growth indicates that the standard deviation was greatest in the low density stands and the coefficient of variation was greatest in the highest density stands. All treatments experienced marked reductions in proportional growth in 1974, 1977, 1981, 1989, 1996, 2000, 2002 and 2006, corresponding with years of lower than average precipitation and wet degree days, and spikes in hot-dry stress. The years 1981, 1996 and 2006 are marked by high temperatures (in the greatest 10% for the observed period).

3.1 | Effects of stand density on soil moisture (objective 1)

Simulated soil moisture captured the observed seasonal and density-dependent patterns of soil moisture observed (Figure 2). Differences

TABLE 2 Mean and variability of annual, stand-level forest growth within each density treatment. Density treatments (low, medium, high and control; top to bottom) refer to ponderosa pine stands with basal areas of 9, 23 and 34 m²/ha, and an untreated control plot

Treatment	Mean	SD	CV	Range
BAI (m ² ha ⁻¹ year ⁻¹)				
Low	0.249	0.120	0.481	0.646
Medium	0.429	0.114	0.266	0.635
High	0.631	0.192	0.305	1.016
Control	0.645	0.239	0.371	1.199
Proportional growth (BAI/BA)				
Low	0.028	0.009	0.319	0.049
Medium	0.020	0.006	0.309	0.044
High	0.019	0.007	0.387	0.041
Control	0.014	0.006	0.404	0.025

Abbreviations: BA, basal area; BAI, basal area increment.

between simulated and observed moisture, in particular the spring of 2015–winter of 2016 and the spring of 2016, may be a result of discrepancies between actual precipitation, which we do not have, and gridded weather data used in the simulations. The relationship between stand density and soil moisture varied by depth in the soil profile and by time of the year (Figure 3). Overall, soils in each treatment were wettest in March and April and driest in late May and June (Figure 3a). Treatment differences in soil moisture were most pronounced in the deepest soil layers (80–100, 100–150 cm) in the driest time of the year (mid-to-late June). These differences were negative in the control treatment, indicating drier conditions, and positive in the low density treatment, representing wetter conditions. While the most marked difference was in the deep soil layers, drier and wetter patterns were noticeable throughout all layers from April through June. Additionally, differences were observed in late August through October in shallow and intermediate soil layers (10–80 cm), with the lowest density treatment drier than average, and the medium BA and control wetter (Figure 3b).

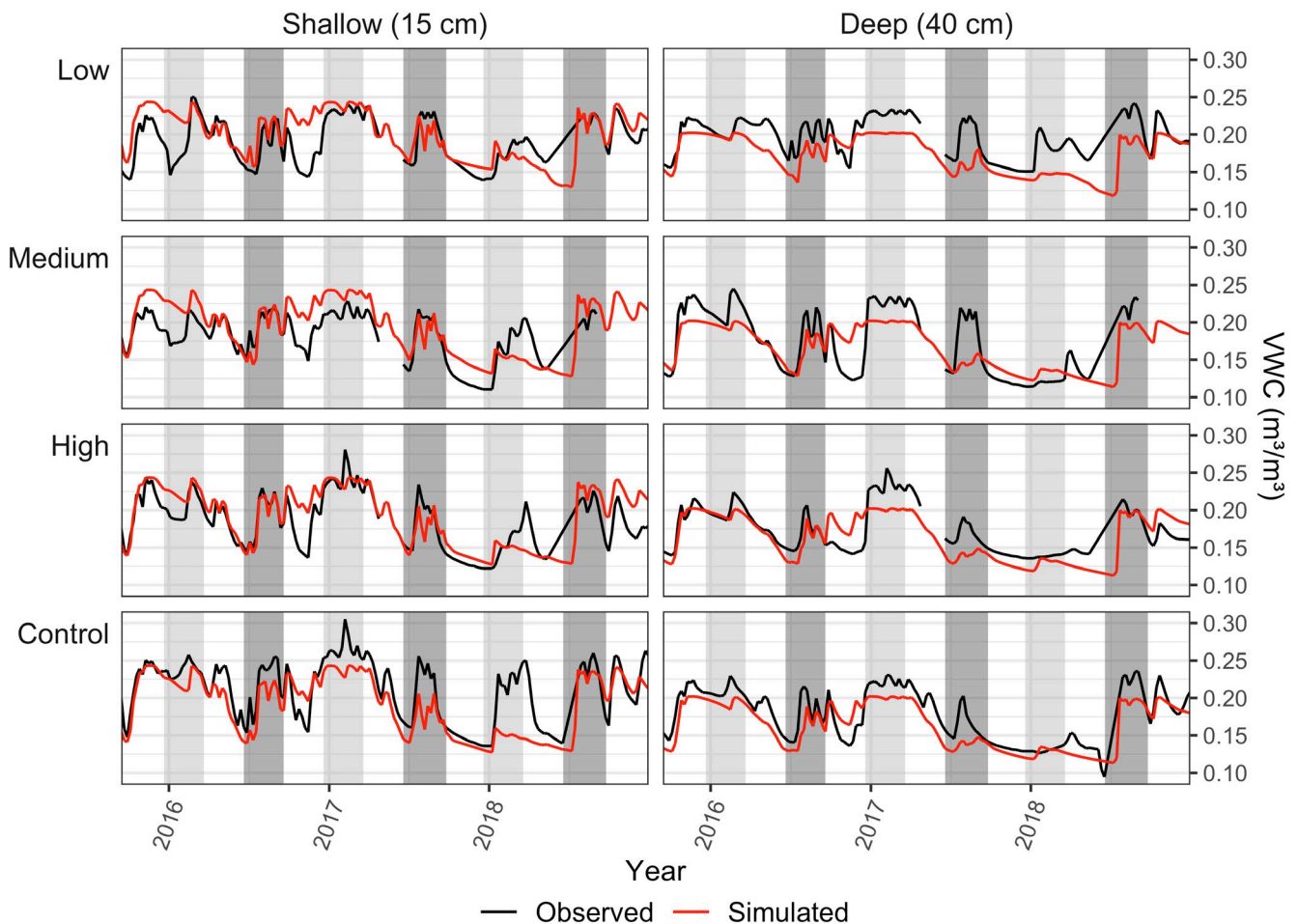


FIGURE 2 Simulated (red) and observed (black) volumetric soil water content (VWC [m³/m³]) for two depths (15 cm [left-hand panels] and 40 cm [right-hand panels]) and four basal area (BA) treatments of ponderosa pine. The four BA treatments are low (9 m²/ha, top panels), medium (23 m²/ha, panels second from top), high (34 m²/ha, panels second from bottom), and control (bottom panels). In each figure winter (December–March) is overlain in light grey and the monsoon (July–September) in dark grey. Observed soil moisture data were collected with 5TM soil moisture sensors at depths of 15 and 40 cm, in one replicate of each treatment, on an hourly basis from September 2015 through December 2018. Simulations were completed with the SOILWAT2 eco-hydrological water-balance model

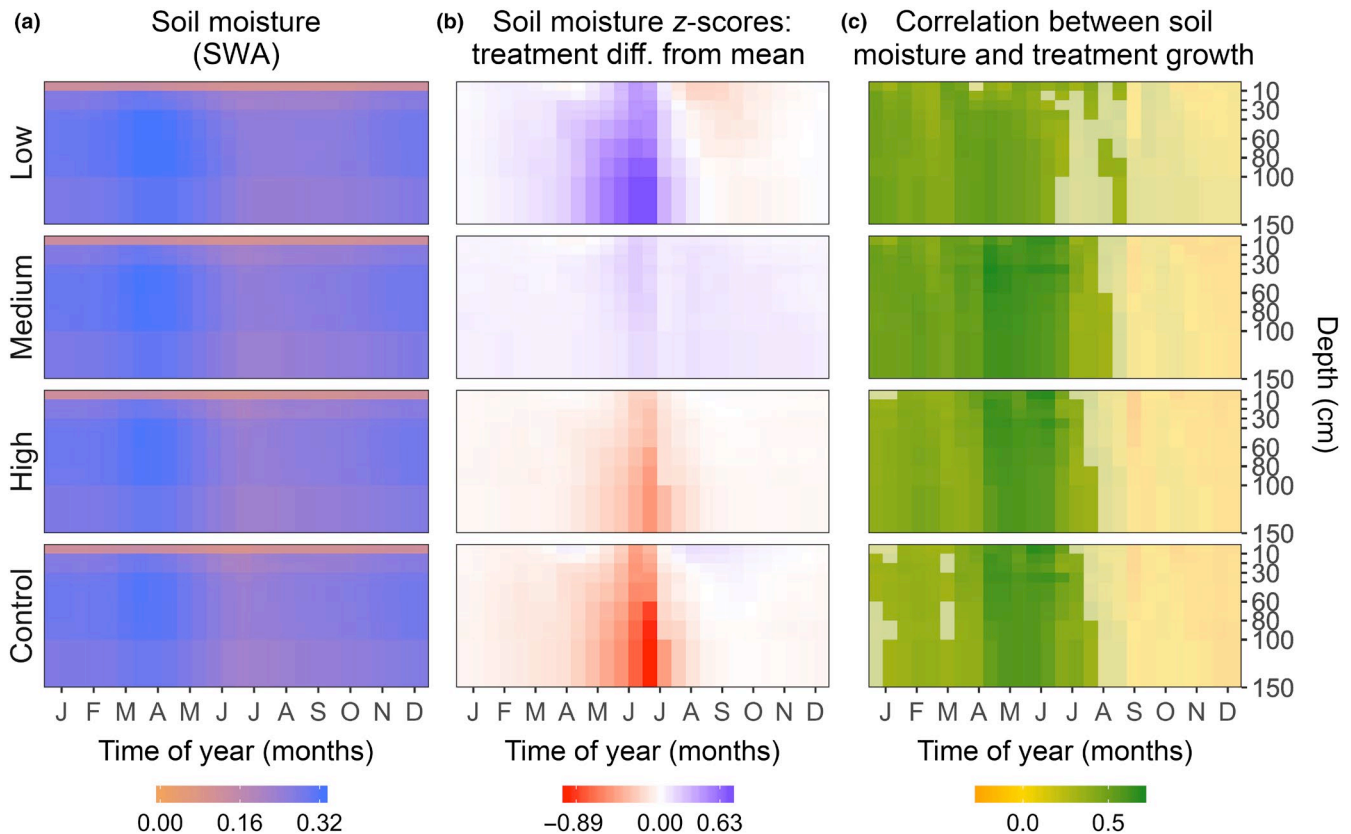


FIGURE 3 Patterns of soil moisture and correlations between soil moisture and growth at Fort Valley Experimental Forest. Density treatments (low, medium, high and control; top to bottom) refer to ponderosa pine stands with basal areas of 9, 23 and 34 m²/ha, and an untreated control plot. Columns are (a) long-term (1972–2011) seasonal mean soil moisture (soil water availability (SWA), cm) by soil depth, (b) variation in SWA among treatments, illustrated by individual treatment z-scores, calculated as the number of standard deviations from the cross-treatment mean, (c) correlation between soil moisture and treatment level growth (BAI, m² ha⁻¹ year⁻¹)

Correlation analysis demonstrated that inter-annual variability of stand-level growth was most positively related to spring (April–June) soil moisture at intermediate depths (Figure 3c) in all density treatments. Soil moisture in the medium density treatment (23 m²/ha) was most positively correlated with inter-annual growth ($r = 0.69$), and the low density (9 m²/ha) treatment was overall less correlated to soil moisture. Correlations of inter-annual growth and soil moisture were non-significant in the late-fall and winter months for all treatments.

3.2 | Ecological drought drivers of forest growth (objective 2)

In general, relative moisture availability is greatest in the winter months (Figure 4a,b) and the greatest hot-dry stress occurs mid-year during June (Appendix S2, Figure S1b). In an average year, wet degree days accumulate slowly in the spring as temperatures become high enough for trees to utilize the water available, and increase rapidly with the onset of the monsoon (July and August, Appendix S2, Figure S1c). The CCP analyses identified the four ecological drought periods with the most significant correlations with growth (Table 3). These include relative moisture availability during the current growing

season (Figure 4c, Moisture_{0ya}, positive correlation) and the previous growing season (Moisture_{1ya}, positive), hot-dry stress accumulated in the previous 2 years (Stress_{2ya}, negative), and the average number of wet degree days in the previous 2 years (WDD_{2ya}, negative).

These four ecological drought periods and three climate measures (annual max temp, annual mean temp and frost-free period) retained through co-correlation reduction, and annual BA were considered in the stepwise model selection process. Our final predictive equation for annual stand-level growth (Equation 1) included BA, relative moisture availability in the current year and the previous year (Moisture_{0ya} and Moisture_{1ya}, respectively), hot-dry stress over the previous 2 years (Stress_{2ya}), and interactions between BA and both Moisture_{0ya} and Stress_{2ya}, as follows

$$\begin{aligned} \text{BAI} = & 0.9822 - 0.0154(\text{AnnualMaxTemp}) - 0.0285(\text{AnnualMeanTemp}) \\ & - 0.00081(\text{BA}) - 0.92219(\text{Moisture}_{0\text{ya}}) + 0.1606(\text{Moisture}_{1\text{ya}}) \quad (1) \\ & + 0.0099(\text{Stress}_{2\text{ya}}) + 0.0922(\text{BA} \times \text{Moisture}_{0\text{ya}}) \\ & - 0.0015(\text{BA} \times \text{Stress}_{2\text{ya}}). \end{aligned}$$

Neither frost-free period nor WDD_{2ya} were selected for inclusion in the final model. The model accounted for a reasonably high proportion of inter-annual growth variability within and among these stands ($R^2 = 0.74$), with no evidence of bias (Appendix S3).

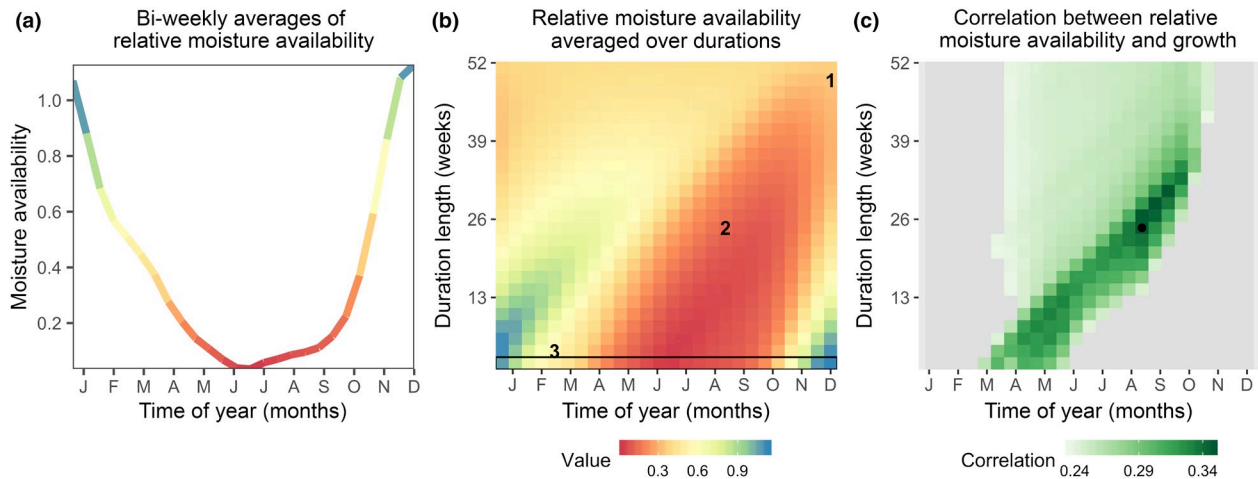


FIGURE 4 Example critical climate period analysis for relative moisture availability. (a) Seasonal, long-term (1972–2010) biweekly average values of relative moisture availability, calculated as the sum of soil moisture (SWA, cm) in all soil layers divided by potential evapotranspiration (cm). Relative moisture availability was calculated across all density treatments and corresponds directly with the lowest row of panel (b), outlined in black. (b) A matrix of relative moisture availability values by time of year and duration length. Values for each duration and time of year (represented by colours) are calculated by averaging moisture availability over increasingly longer time periods (*duration length*, y-axis in b & c) up to 1 year (52 weeks). Each calculation was performed 26 times, ending at various points within a year (x-axis). (c) Correlation between relative moisture availability at each duration-lag time period and annual stand-level growth (BAI, $m^2 ha^{-1} year^{-1}$) across all densities. Only significant correlations are coloured. Periods with non-significant correlations are shaded grey. Numbered arrows below panel (a) illustrate the time periods marked in panel (b); arrow length indicates the moisture availability values averaged. For example, period 1 in panel (b) marks a 50-week duration length and the calculation ends in mid-December. Hence, values of relative moisture availability for the 50 weeks preceding mid-December are averaged and the resulting value represents mean moisture availability for approximately one calendar year. Period 2 is a 26-week time period that ends in late-summer and represents mean conditions from February to August. Period 3 is a short time period representing mean conditions in January and February

TABLE 3 Ecological drought periods selected by the critical climate period and co-correlation reduction analysis

Name	Notation	Variable	Duration (weeks)	Lag (weeks)	Time period	Ecological meaning	Correlation	Selected in final model?
Moisture availability in the current growing season	Moisture _{0ya}	Moisture availability ratio	24	18	Current growing season; late spring through mid-autumn	How much soil moisture is available in the current growing season?	0.4310	X
Moisture availability in the previous growing season	Moisture _{1ya}	Moisture availability ratio	42	54	Previous growing season; spring through autumn	How much soil moisture was available in the previous growing season?	0.2952	X
Long-term hot-dry stress	Stress _{2ya}	Hot-dry stress	46	84	1–2 years prior; starting summer (2ya) through spring (1ya)	How stressful were the previous 2 growing seasons?	–0.1859	X
Long-term wet degree days	WDD _{2ya}	Wet degree days	60	74	1–2 years prior; starting summer (2ya) through summer (1ya)	How wet were the previous two growing seasons?	–0.1182	–

3.3 | Influence of stand density on growth response to ecological drought (objective 3)

Long-term patterns of ecological drought across the density treatments suggest that relative moisture availability displayed very little

variation among treatments, while wet degree days were generally higher in low density stands, and hot-dry stress was generally higher in high density stands (Figure 1f–h). Relationships between proportional growth and the ecological drought conditions selected in Equation 1 illustrate how density modifies the impacts of drought

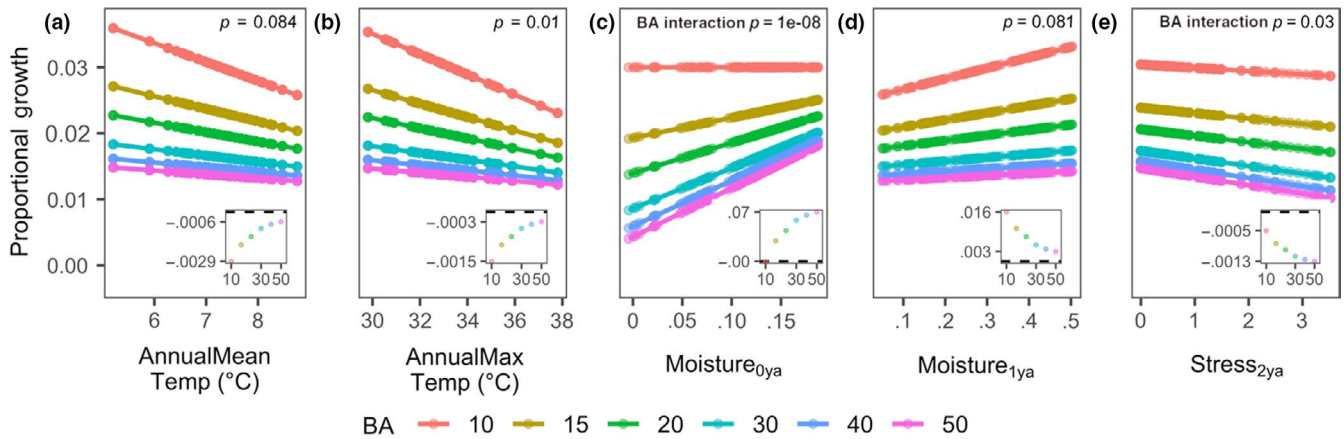


FIGURE 5 Predicted proportional growth (basal area increment [BAI, $\text{m}^2 \text{ha}^{-1} \text{year}^{-1}$]/basal area [BA, m^2/ha]) estimated in response to each independent variable included in the final linear regression model for several levels of stand basal area. Growth was derived from Equation 1, holding other variables at their mean and calculating growth across a range of values for the focal variable (x-axis) at different levels of stand basal area. p -values for each variable (or the interactions between the variable and basal area) are shown in the top-right corners. Full model output is included in Appendix S3, Table S1. Insets: Slope of the relationship in the main panel for each BA level. Dashed vertical line in the inset designates no relationship (i.e. zero slope). Stress refers to hot-dry stress

and temperature on growth (Figure 5; Appendix S4, Figure S1). Specifically, as BA decreases there was generally greater overall moisture availability ($\text{Moisture}_{0\text{ya}}$, $\text{Moisture}_{1\text{ya}}$) and less intense hot-dry stress ($\text{Stress}_{2\text{ya}}$), resulting in greater proportional growth in lower density stands.

The direction of the influence of temperature and ecological drought on stand-level growth is consistent across stand density, but the sensitivity of growth to variation in temperature or drought varies by density. Specifically, growth was negatively related to temperature (Figure 5a,b), and growth response to temperature was greater in lower density stands. Growth was positively related to both relative moisture availability metrics. Growth sensitivity to relative moisture availability in the current year ($\text{Moisture}_{0\text{ya}}$; Figure 5c) varied widely among densities, with the low density showing little to no sensitivity and the high density stands demonstrating a large amount of variation in response to increasing current growing season moisture. By contrast, growth sensitivity to relative moisture availability in the past year ($\text{Moisture}_{1\text{ya}}$; Figure 5d) was reasonably consistent among treatments, although the low density stand appeared to be slightly more sensitive than other treatments to variation in $\text{Moisture}_{1\text{ya}}$. Growth was negatively related to hot-dry stress, with little variation among densities (Figure 5e), although the higher densities displayed a slightly more negative response.

4 | DISCUSSION

Climate change in the 21st century is expected to increase the frequency and severity of hot drought events that decrease forest growth and increase tree mortality. Understanding how stand density moderates the response between forest growth and drought can help foresters devise silvicultural actions that will mitigate these threats. Here, in the first study of its kind, we combined replicated manipulations of density with soil moisture estimates to directly

examine how density itself influences moisture availability and how this, in-turn, affects growth rates, particularly during hot-dry events. Numerous indices have been used to examine the impacts on moisture stress on tree growth, including PDSI and SPEI (Bottero et al., 2017; Gleason et al., 2017); however, a key limitation of these approaches has been the inability to account for the influence of stand-level density on seasonal patterns of soil moisture, as well the interactions between density, soil moisture availability and atmospheric moisture demand over extended periods of forest development. To address these limitations, we developed new ecological drought metrics of moisture availability and hot-dry stress that explain inter-annual variability in dry forest growth. Our ecological drought metrics, combined with critical climate period analyses, identified specific timing and duration of moisture availability and hot-dry stress that influence forest growth.

4.1 | Effects of stand density on soil moisture

The benefits of using soil moisture as our water availability metric, in lieu of the more traditional measures of drought, are two-fold. First, patterns of available soil moisture are determined by potentially complex interactions among temperature, precipitation amount and seasonality, edaphic conditions, and vegetation structure. We attempted to represent these factors, explicitly estimate the amount of water available for utilization by the root systems of ponderosa pine, and identify the times and depths when moisture availability are most crucial for growth. The drought metrics based on these important characteristics of moisture availability provide an ecologically relevant focal point for considering long-term climate change impacts. Second, stand density itself directly influences soil moisture through a number of eco-hydrological processes (Bréda et al., 2006; Simonin, Kolb, Montes-Helu, & Koch, 2007), and inspecting precipitation or traditional drought indices, such as PDSI or SPEI

alone, would not provide insight into the influence of altered stand structure on moisture availability. Quantifying the interactive relationship between density and soil moisture allows forest managers to understand how density manipulations impact drought stress, growth and long-term resilience indicated by sustained growth even in drought conditions.

Patterns of soil moisture, both seasonal timing and depth (in the soil profile), among density treatments are consistent with our expectations of water balance given the variation in vegetation structure in these stands. In support of our first hypothesis, we found that soils in the lower density stands were typically wetter throughout the first half of the year, and most noticeably at deeper depths during the driest time of the year (May–June). Greater wetness in the soil profile throughout the winter and into spring can be attributed to more precipitation and less evaporative demand in the winter, and snowmelt in the spring. This is consistent with previous work that has shown larger trees in low density stands are deeper rooted and are able to take advantage of this deep soil moisture that is recharged in the winter months (Kerhoulas, Kolb, & Koch, 2013). The marked difference in wetness during May and June, corresponds with the timing of the greatest amount of tree transpiration (Appendix S5). Transpiration is positively related to density and the corresponding increase in leaf area index (Bréda et al., 2006). Transpiration draws water from the soil profile to a depth of at least 170 cm in ponderosa pine systems (Berndt & Gibbons, 1958). Increased relative dryness in low density stands in the shallow and intermediate soil layers during late summer is an effect of greater evaporation in these stands both due to less canopy cover and greater exposure of the ground to the effects of solar radiation (Simonin et al., 2007), but also to the presence of an graminoid understory that is absent from higher density stands (Flathers, Kolb, Bradford, Waring, & Moser, 2016). These shallower-rooted grassy species in the understory are more effective than trees at utilizing pulse, monsoon moisture events that comes when atmospheric demand is high in the summer (Schwinning & Sala, 2004).

4.2 | Ecological drought drivers of forest growth

We identified three ecological drought metrics that explain patterns of stand-level growth. Consistent with our second hypothesis, the drought metrics that most explained growth (moisture availability ratio and hot-dry stress) both integrated the effects of both temperature and soil moisture. Wet degree days, a metric with no penalty for high temperatures, was not selected for the final model. We also found that forest growth responds to ecological drought and temperature conditions in the current growing season, and up to 2 years prior to measurement. Prior research has identified techniques to quantify the 'ecological memory' of an ecosystem, accounting for the seasonal timing, lags, and strength of these relationships including stochastic antecedent modelling (Ogle et al., 2015). Yearly lags in climate response are commonly identified as drivers of wood formation in temperate and boreal tree species, particularly determinate

species (Camarero et al., 2018); however, our findings suggest an even greater duration of drought effects for dry forests. Our model suggests that forest growth is highly responsive to moisture availability in both the current and previous growing seasons, as well as hot-dry stress accumulated over a period beginning 2 years prior. These results are consistent with previous findings evaluating the relationship between growth and drought for pine species in the USA (D'Amato et al., 2013; Williams et al., 2013), but highlights periods that were selected without any a priori expectations. The impact of such observed drought legacy effects are varied, with reduced tree-ring growth not always resulting in the loss of other plant and ecosystem functioning such as photosynthesis and gross primary productivity (Kannenberg et al., 2019), but has been linked with mortality via hydraulic damage and eventual cavitation (Anderegg et al., 2013).

Previous evaluations of the effects of moisture and temperature on growth have often focused on tree-level response to periods of known drought (Berdanier & Clark, 2016; Bréda et al., 2006). While this strategy characterizes the specific conditions of drought vulnerability, it does not account for the suite of circumstances that could also be beneficial to overall stand growth. Silviculture is applied to stands and as such most restoration and climate adaptation treatment plans are applied at the stand-level, highlighting the utility of a model that captures stand-level growth over a range of potential densities. Our stand-level results are important in the context of climate change, as most objectives associated with long-term adaptation are not merely focused on managing trees to avoid catastrophic failure, but also aspire to sustain stand-level growth. Furthermore, a model of this type can be used to make annual predictions of what growth might look like under various climate and density scenarios. Lastly, because the model includes terms that explicitly represent soil moisture availability, it can incorporate the effects of soil texture and depth, providing a detailed perspective on landscape patterns in drought vulnerability.

4.3 | Influence of stand density on growth response to ecological drought

Our unique modelling approach and results provide new insight on how soil moisture and temperature conditions interact with stand density to influence forest growth. As we hypothesized, high density stands appeared especially sensitive to hot-dry stress and moisture availability during the current growing season. However, low density stands were more sensitive to moisture availability during the previous year. Relatively low growth sensitivity in low density stands to current year's relative moisture availability ($\text{Moisture}_{0\text{ya}}$) versus high sensitivity to previous year's relative moisture availability ($\text{Moisture}_{1\text{ya}}$), suggests that the low density stands are sustaining growth during unfavourable years by utilizing stored carbohydrates from previous years (O'Brien, Leuzinger, Philipson, Tay, & Hector, 2014). Additionally, the larger trees present in these low density stands likely have deeper root systems and may rely on deep soil water storage supplied from earlier years (Kerhoulas, Kolb, & Koch, 2013). By contrast, the high density stands

are extremely sensitive to $\text{Moisture}_{0\text{ya}}$ and relatively unresponsive to $\text{Moisture}_{1\text{ya}}$, perhaps indicating that these stands are unable to build a carbohydrate reserve even during good years, or lack deep soil water recharge as well as the ability to access it, resulting in dramatically low growth during unfavourable conditions. Our final model was selected by forward stepwise selection and thus may have avoided including additional terms that could enhance model performance. Nevertheless, the model still explained 74% of the variability in annual tree growth, and our parsimonious final model derived from this conservative approach may be more appropriate for developing long-term projections of forest growth under climate change than a more complex model. It is also important to note that overall, model fit was better for growth in the higher density than lower density stands (Appendix S3, Figure S1). This suggests that growth in low density stands is not as limited by moisture, likely because there is more moisture overall and/or because these larger, deeper-rooted trees can access deep water resources.

Predictions from our model indicate that higher temperatures displayed consistent negative relationships with growth. Temperature impacts on growth were largest in low density stands with substantial inter-annual variability in growth, and smallest in high density stands that have low and relatively unvarying growth patterns. However, low density stands displayed substantially higher long-term average proportional growth than higher density stands, and maintained higher proportional growth even when temperatures were high. This is important given that climate models for the southwestern USA consistently agree that temperatures will increase in the coming century (Cook et al., 2015) and that warmer conditions during drought have been shown to hasten mortality in stands composed of pine (*Pinus* spp.; Breshears et al., 2018; McDowell et al., 2019).

5 | CONCLUSIONS

It is important to note that this analysis used long-term density experiments that do not perfectly represent the complex mosaic of individual trees of various sizes, clumps, and openings that characterized historical spatial arrangements in dry ponderosa pine ecosystems (White, 1985), nor the actual tree spacing objectives of many forest restoration treatments (Churchill et al., 2013), where variable density thinning and multi-aged forest structure are emphasized (Reynolds et al., 2013). While it is not clear exactly how spacing would influence the drought response, our results do provide insight into interactions between density and drought that will be important to understand in coming decades. Additionally, the modelled relationship between growth and ecological drought was developed based upon observations of historical climate conditions and utilized linear relationships between growth and drought. While our model accounted for 74% of growth variation, the linear relationships may limit the model's accuracy under future conditions. Our estimates of growth also do not consider potential threshold responses of mortality. For example, paleo-reconstructions have found that ponderosa pine distribution has decreased with decreasing July precipitation (Norris, Betancourt, & Jackson, 2016).

Despite these limitations, our finding that proportional growth in low density stands is greater than that in high density stands during hot temperature events implies a clear benefit of thinning for a warming 21st century, as noted by others (Kerhoulas, Kolb, Hurteau, & Koch, 2013). To evaluate the broader representativeness of this research, we determined the aridity class of forests world-wide, in order to determine the extent

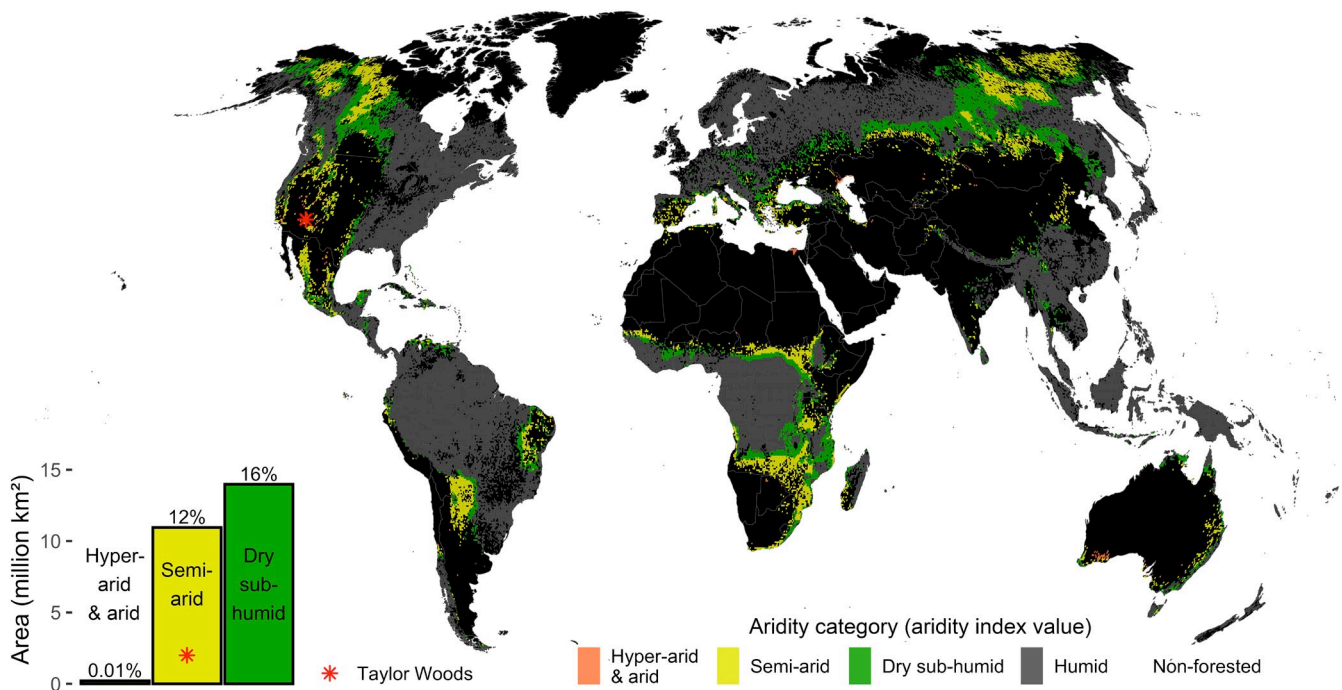


FIGURE 6 Map and bar chart (inset in bottom left) of forests world-wide categorized by aridity category (as defined by UNEP, 1997). The location and aridity of our study site, Taylor Woods, is shown with a red star. Values in the bar chart are the percent of total of forested land (area in km²) by aridity class. 71.7% of forested land is in the humid aridity class (not included in bar chart)

and location of other forested ecosystems where growth might be water limited. Forest data were provided by Hewson, Crema, González-Roglich, Tabor, and Harvey (2019) and aridity data by Trabucco and Zomer (2018), both at an approximate 1 km scale. This benefit is relevant for forests across a broad range of aridity conditions (Gleason et al., 2017), and particularly for the ~28% of global forests (25.2 million km²) that occur in in dry sub-humid, semi-arid or drier conditions (Figure 6). Density reduction in dry forest ecosystems not only sustains growth and boosts resilience to drought, but also produces many co-benefits that increase overall ecosystem health, including resistance and resilience to wildfire (Ziegler et al., 2017), decreased susceptibility to insect outbreak (Kolb et al., 2016), increased regeneration (Kolb et al., 2020) and decreased risk of mortality during drought events (Breshears et al., 2018), benefits that are likely to become even more important as temperatures rise and hydro-logic regimes shift in coming decades (Bradford & Bell, 2017; McDowell et al., 2019).

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AUTHORS' CONTRIBUTIONS

J.B.B., A.W.D., B.P. and S.F. conceived the ideas and designed methodology; C.M.A., A.W.D., B.P., J.B.B., S.F. and M.A.B. collected the data; C.M.A., J.B.B. and S.F. analysed the data; C.M.A. and J.B.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data generated during this study are available at USGS ScienceBase-Catalog <https://doi.org/10.5066/P9ESPL41> (Andrews et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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