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Increasing radial growth in old-growth high-elevation conifers in Southern California, USA, during the exceptional "hot drought" of 2000–2020

Paul A. Knapp¹ · Peter T. Soulé² · Tyler J. Mitchell¹ · Avery A. Catherwood¹ · Hunter S. Lewis¹

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Abstract

Hot droughts, droughts attributed to below-average precipitation and exceptional warmth, are increasingly common in the twenty-first century, yet little is known about their effect on coniferous tree growth because of their historical rarity. In much of the American West, including California, radial tree growth is principally driven by precipitation, and narrow ring widths are typically associated with either drier or drought conditions. However, for species growing at high elevations (e.g., Larix lyalli, Pinus albicaulis), growth can be closely aligned with above-average temperatures with maximum growth coinciding with meteorological drought, suggesting that the growth effects of drought span from adverse to beneficial depending on location. Here, we compare radial growth responses of three high-elevation old-growth pines (Pinus jeffreyi, P. lambertiana, and P. contorta) growing in the San Jacinto Mountains, California, during a twenty-first-century hot drought (2000-2020) largely caused by exceptional warmth and a twentieth-century drought (1959–1966) principally driven by precipitation deficits. Mean radial growth during the hot drought was 12% above average while 18% below average during the mid-century drought illustrating that the consequences of environmental stress exhibit spatiotemporal variability. We conclude that the effects of hot droughts on tree growth in high-elevation forests may produce responses different than what is commonly associated with extended dry periods for much of western North America's forested lands at lower elevational ranges and likely applies to other mountainous regions (e.g., Mediterranean Europe) defined by summer-dry conditions. Thus, the climatological/biological interactions discovered in Southern California may offer clues to the unique nature of high-elevation forested ecosystems globally.

Keywords Hot drought · Sugar pine · Jeffrey pine · Lodgepole pine · San Jacinto Mountains · Southern California · USA

Introduction

While the general expectation is that drought impacts forest ecosystems negatively, that is not always the case. Multiyear drought conditions are common in Southern California having occurred in 10 of the 13 decades since 1900 and have substantially increased in duration and intensity during the twenty-first century (Soulé and Knapp 2024), mirroring

Paul A. Knapp paknapp@uncg.edu

¹ Carolina Tree-Ring Science Laboratory, Department of Geography, Environment and Sustainability, University of North Carolina Greensboro, Greensboro, NC, USA

² Appalachian Tree Ring Lab, Department of Geography and Planning, Appalachian State University, Boone, NC, USA cipitation) and demand (i.e., evapotranspiration) of moisture and is standardized to reflect climatic normals for a given region (Palmer 1965; Soulé 1992). Drought conditions thus can be generated by persistent heat, extended dryness, or a combination, the latter being a "hot drought" (e.g., De Boeck and Verbeeck 2011; Overpeck 2013; Udall and Overpeck 2017; Cheng et al. 2019; Soulé and Knapp 2024), which has driven the severe, and likely anthropogenically assisted, drought in much of California over the past two decades (Williams et al. 2020). The ecological effects of drought, however, are complex producing "whole-community responses" with some species increasing in abundance while others decrease (Prugh et al. 2018). These responses are affected by several interactive mechanisms including the

global trends (Chiang et al. 2021). Drought conditions are often defined by the Palmer Drought Severity Index (PDSI), a water balance-based metric that factors in supply (i.e., preextreme-event timing of heat waves and droughts (De Boeck et al. 2011) trait groups (e.g., annual and perennial species, above- and below-ground productivity), scale, ranging from plant to ecosystem level, duration, and compound events initiating other disturbance (e.g., prolonged heat and drought-initiated insect outbreaks) (Seaton et al. 2015; Breshears et al. 2021; Ma et al. 2023).

Despite widespread evidence of twenty-first-century drought-related mortality within coniferous forests of California, USA (e.g., Young et al. 2017; Dong et al. 2019; Goulden and Bales 2019), the adverse effects of extreme dryness on tree growth are spatially inconsistent (e.g., Robinson et al. 2023). Here, we discuss how the enhanced radial growth rates of three long-lived coniferous species growing in the San Jacinto Mountains of Southern California coincided with a severe, multi-decadal drought (2000–2020) that represents the driest period since at least 800 CE in southwestern North America (Williams et al. 2022). We posit that the proportionality of precipitation and temperature deviations that generate drought is critical and may generate differential tree growth responses depending on location and a species' elevational range distribution.

Methods

We collected tree-ring data from three long-lived pine species (Pinus jeffreyi, Jeffrey pine, hereafter PIJE and P. lambertiana, sugar pine, PILA in summer 2021, and P. contorta ssp. murrayana, lodgepole pine, PICO in summer 2022) at elevations between 2300 and 2800 m a.s.l. within Mount San Jacinto State Park (MSJSP) in the San Jacinto Mountain (SJM) Range (33.7° N, 116.7° W), one of the Peninsular Ranges of Southern California, USA. MSJSP is roadless, an area of historically minimal human agency (e.g., logging, domestic livestock grazing), and supports approximately 57 km² of old-growth coniferous forest growing under a Mediterranean climate regime (Köppen Csc) with cold, wet winters and cool, dry summers. Climate data (1966–2000) from Long Valley Ranger Station (LVRS) at 2554 m elevation inside MSJSP show mean annual precipitation at LVRS is 600.4 mm with an average of 2166 mm snowfall/year. Mean minimum/maximum temperatures (°C) for January and July are -5.8/8.7 and 6.1/23.5. The soil type (https://websoilsur vey.nrcs.usda.gov/app/WebSoilSurvey.aspx) is composed of weathered granodiorite residuum with a soil profile of gravelly sandy or coarse sandy loam to a depth of 64 cm overlaying a weathered bedrock. We sampled two cores per tree for at least 30 trees for each species and processed them following standard dendrochronological methods (Stokes and Smiley 1996) and confirmed crossdating accuracy using COFECHA (Holmes, 1983). We standardized (mean = 1) and detrended each totalwood chronology for age-related growth response using negative exponential detrending in the program ARSTAN (Cook and Krusic 2005) and retained the STANDARD output for each species and the raw ring widths (mm).

To determine climate/radial growth responses, we examined monthly precipitation, PDSI, and minimum, maximum, and average temperature data for the South Coast Drainage Climate Division of California (Climate Division CA6; hereafter CD6) during 1900-2020. Temperature and precipitation values between the CD6 and LVRS data sets are significantly related (p < 0.01), but because the LVRS data were incomplete (e.g., missing observations for multiple years) and represented a shorter period, we used the CD6 data for our analyses. As a surrogate for snowpack, we used data from the LVRS showing the Julian date of the last day of snow cover, beginning in 1967 and ending in 2020 with 6 total years of missing data including 5 years since 2020. We used PDSI values to characterize long-term (i.e., multiyear) drought conditions as this metric is commonly used for dendroclimatic studies (e.g., Kerhoulas et al. 2017; Tran et al. 2017; Montpellier et al. 2019; Gangopadhyay et al. 2022) and has been demonstrated to exhibit the highest correlations of water availability variables with radial growth of pine species in the Southwestern USA (e.g., Kempes et al. 2008; Keen et al. 2020; Keen et al. 2022). We defined a drought event as any period with three or more consecutive months with PDSI values < -2 (qualitatively "moderate drought"), a metric first proposed and used by Diaz (1983). We tabulated the number of drought events, mean length (months), and mean severity of drought events. We correlated climate/growth relationships using Pearson correlation and compared differences in radial growth between the longest twentieth-century multi-year drought (1959-1966) with the hot drought period of 2000-2022 using an independent samples test. Lastly, to facilitate the evaluation of annual temperature and precipitation deviations during the two drought periods, we converted mean minimum temperature and total precipitation to z-scores based on the 1900-2020 CD6 data.

Results and discussion

Mean radial totalwood growth (i.e., standardized ring-width indices) during 2000–2020 (PDSI $\bar{x} = -2.17$) was 1.07 (PIJE), 1.17 (PILA), and 1.13 (PICO) with a group average of 1.12 or 12% above the 300–400-year-long chronologies (Fig. 1 A–D, Table 1). However, during 2011–2020 (PDSI $\bar{x} = -3.22$), which included the most severe portion of the twenty-first-century drought marked by 85 consecutive months of negative PDSI values ($\bar{x} = -4.98$), radial growth averages were 1.24, 1.38, and 1.20 with a group average of 1.27 or 27% above average. In comparison, during an earlier

Fig. 1 A–C Standardized radial growth (green), raw-ring widths (red, mm) of totalwood, and chronology sample depth (black) for PIJE (**A**), PILA (**B**), and PICO (**C**). **D** Annual precipitation (blue), annual minimum temperature (red), and number of months per decade (black and shown at the end of the decade) with PDSI values <-2. Climate data are from CA CD6



Table 1 🛛 🕅	Results for chronology	development, radial	growth, and climate	e metrics for PIJE, PILA	A, and PICO
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Species	PIJE	PILA	PICO	Group mean
Series intercorrelation	0.65	0.66	0.63	
Mean Sensitivity	0.25	0.27	0.23	
Standardized mean totalwood growth 2000-2020	1.07	1.17	1.13	1.12
Mean PDSI (2000–2022)	-2.17	-2.17	-2.17	-2.17
Standardized mean totalwood growth 2011-2020	1.24	1.38	1.2	1.27
Mean PDSI (2011–2022)	-3.22	-3.22	-3.22	-3.22
Standardized mean totalwood growth 1959-1966	0.76	0.88	0.83	0.82
Mean PDSI (1959–1966)	-1.91	-1.91	-1.91	-1.91
Earlywood width (%) of totalwood raw ring widths	80.1	85.1	86.3	83.3
Correlation with mean annual (prior Nov–current Oct) minimum temperature. All values ($p < 0.01$)	0.61	0.46	0.55	
Correlation with total annual (prior Nov–current Oct) precipitation. All values ($p < 0.01$)	0.39	0.27	0.34	
Correlation with date of spring snow melt 1967–2020. Significant at $p < 0.05$ for PIJE and PICO	0.34	0.16	0.34	

period (1959–1966) characterized by persistent drought (PDSI $\bar{x} = -1.91$), which included 54 consecutive months of negative PDSI values ($\bar{x} = -3.05$), mean radial totalwood growth was 0.76, 0.88, and 0.83 with a group mean of 0.82, indicating growth was 82% of average (Table 1). The mean radial growth of PIJE, PILA, and PICO and the three species combined during 2000–2020 was significantly greater (p < 0.01, 0.05, 0.01, 0.01) during the hot drought period of 2000–2020 compared to the 1959–1966 drought. Similarly, mean radial growth was significantly greater (p < 0.01) during 2011–2020 than 1959–1966 for each species and all species combined (Table 1).

From the mid-twentieth century through 2020, radial growth was most strongly related to annual (November–October) minimum temperature (r = 0.61, 0.46, and0.55, p < 0.01) and secondarily by annual (November–October) precipitation (r = 0.39, 0.27, 0.34, p < 0.05); thus, temperature is the principal driver of growth and trees respond positively to warmth (Table 1). Two narrow growth outlier years since 2000 (2007 and 2002) were the two driest years (z-scores -1.66, -1.61) since 1900, yet radial growth during 2014 and 2018, which were the fourth and fifth driest years (z-scores of -1.45, and -1.30), were 1.25 and 1.25, or collectively 25% above average. The principal difference between the low-growth outliers of 2002 and 2007 and the above-average growth of 2014 and 2018 is that the later years were the second (tied) warmest since 1900 (z-scores 3.62) while 2002 was the 47th warmest (z-score 0.22) and 2007 was the 27th warmest (z-score 0.69). The 1959–1966 and 2000-2020 droughts differ as the earlier drought was marked by cooler (-0.47 °C) and much drier (-109 mm) conditions (1900-2020 means of 8.87 °C and 431 mm) in contrast to the 2000-2020 hot drought, which was warmer (0.6 °C) and drier (-43.9 mm)—a drought type that has not otherwise affected Southern California since 1900 (Fig. 1D). Raw ring widths either significantly (p < 0.05) increased (PIJE and PILA, Fig. 1A and B) or remained stable (PICO, Fig. 1C) during 2000–2020 indicating increases in standardized growth were not a mathematical result of narrowing ring widths.

We found no evidence that increased radial growth during the twenty-first century was associated with changes in chronology depth, tree age, or changes in springtime snow cover duration (i.e., timing of the snowmelt). Specifically, (1) among the three chronologies used to compare the two drought periods, 82 of the 86 samples covered both periods, (2) the mean (range 215-255 years) and median (range 228-271 years) ages of the cores used for comparison suggest growth changes were not associated with major lifestage shifts, and (3) there was not a shift (r = -0.08, p =0.54, n = 48) in snow cover duration. Several (e.g., Vaganov et al. 1999; Sanmiguel-Vallelado et al. 2021) have documented that delayed melt of snowpack is associated with delayed soil warming and thus a later onset of tracheid production. However, we found springtime snowmelt timing was positively correlated with radial growth for PIJE and PICO (r = 0.34, p < 0.05 for both species), but not for PILA (p > 0.05) suggesting that years with later snowmelt dates did have a minor to non-existent influence for these species growing in MSJSP (Table 1).

Conclusions

We found three pine species experienced increased radial growth during the extended hot drought of 2000–2020, except during 2002 and 2007, suggesting there are limitations to above-average growth during hot droughts only under the most extreme drought conditions. In this Mediterranean climate environment, radial growth for each species is principally earlywood, comprising > 80% of the total raw ring widths (Table 1), and these ratios

remained stable during the study period. We posit that outside of extremely low precipitation years, the effect of hot droughts on tree growth at high elevations in the SJMs and likely elsewhere with similar conditions in western North America where temperature is the principal growth driver is to advance the onset of cambial growth to earlier in the summer because of an elongated earlywood growing season. Our conclusion is consistent with dendroclimatic studies of conifers at high-elevation sites in Montana, USA, including Kichas et al. (2023) who documented increased radial growth of P. albicaulis under warmer and drier conditions and that of Knapp and Soulé (2011) who found that maximum Larix lyalli growth occurred during periods of summer meteorological drought. Conversely, in an evaluation of two pine species (P. sylvestris and P. halepensis), Camarero et al. (2022) found that an association between a longer growing season and enhanced radial growth was complex and for P. sylvestris growing at a boreal site, radial growth did not increase despite an earlier onset of leaf and wood formation. Thus, increased twenty-first-century growth of the three pine species we examined may reflect either faster growth or a combination (i.e., increased growing season length and rate) of these factors. Conversely, radial growth differences between the early and late drought periods are unlikely an artifact of (1) tree mortality occurring during the first drought period resulting in only heartier, faster-growing trees included in the chronology during the "hot drought" period, (2) changes in mean/median tree ages from juvenile to adult stage, and (3) changes in snow cover duration in MSJSP.

The greatest mortality reported for coniferous species of California during the extended drought has been associated with trees growing on lower-elevation western slopes of the southern Sierra Nevada (Fettig et al. 2019; Madakumbura et al. 2020) and Transverse and Peninsular Ranges of Southern California (Dong et al. 2019). In these environments, trees have been more susceptible to extensive drought because of overall drier and warmer conditions resulting in severe drought. During these hot droughts, the effects of meteorological conditions on growth are detrimental as opposed to beneficial although exceptions, principally highelevation forests such as found in the SJMs, exist where species are growing at their mid-to-upper elevational limits and generally are not water-limited. Thus, it is not that trees grow faster during droughts, but rather when increasing temperatures promote hot drought conditions that exceptional growth conditions can occur in some temperature-limited environments including the SJMs. Lastly, multiyear hot droughts are likely to increase in the twenty-first century, which may influence tree selection criteria when choosing species for climate reconstructions as climate/growth responses of the twentieth century can differ from the twenty-first century depending on location.

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Data Availability Data from this study are available from the corresponding author upon reasonable request.

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