https://doi.org/10.17221/191/2020-JFS

Tree-ring climate response of Jeffrey pine in the Cascade Creek Watershed, Northern California

Raju Bista, Michelle Mohr, David Saldaña, Gabriel Angulo,*
Parveen K. Chhetri

Department of Earth Science and Geography, California State University Dominguez Hills, Carson, California, USA

**Corresponding author: rbista1@toromail.csudh.edu*

Citation: Bista R., Mohr M., Saldaña D., Angulo G., Chhetri P.K. (2021): Tree-ring climate response of Jeffrey pine in the Cascade Creek Watershed, Northern California. J. For. Sci., 67: 285–297.

Abstract: Understanding the forest response to ongoing climate change is crucial in forest management strategies under anticipated climate adversity. To understand the retrospective growth dynamics of Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), tree-ring chronology from the subalpine forest in the Lake Tahoe Basin, California was correlated with air temperature, precipitation, and Palmar Drought Severity Index (PDSI). The years 1757, 1782, 1886, 1859, 1876, 1920, 1929–30, 1977, 1988–89, 2001–02, 2008, and 2014 were some of the years with noticeable low growth. There was robust growth in 1747–49, 1792, 1828, 1866–68, 1913, 1969, 1984, 1998, and 2011. Ring width index (RWI) and basal area increment showed a recent growth increase. Climate-growth response analysis revealed the growth-inhibiting influence of the hot and dry summer. More pronouncedly, warm and wet winter was found to be conducive to tree growth in the following year. A significant growth correlation with the previous year climate (stronger with PDSI) and its absence in current spring may be suggestive of potential growth stimulation by predicted warmer and longer growing season in the future. However, since the RWI chronology consisted mostly of mature trees and because the old cambial age tends to have signal divergence, further studies incorporating younger trees and cohabitant species would provide deeper insights into the growth-climate response.

Keywords: basal area increment; drought; growth-climate correlation; radial growth; ring width index

Understanding the forest ecosystem response to changing climatic conditions is the burgeoning concern and urgency that plant scientists and forest managers have. Moreover, spatial and temporal heterogeneities in the changing patterns and varying responses of different species further complicate comprehending how forests will respond to future environmental changes (Williams et al. 2010). Plants limited by low temperature, particularly in high latitude and high altitude areas (Millar et al. 2004; Salzer et al. 2009), may be favoured by warming. In contrast, warming amplifies drought in low precipitation areas reducing the productivity of the forest ecosystem and increasing tree mortality (Allen et al. 2010). In xeric environments, increased temperature intensifies atmospheric water demand and lowers tree's hydraulic conductivity in physiological response (Babst et al. 2018), thereby hampering structural growth and productivity. In the continuum of anticipated frequent, longer, and severer drought and heat stress (Van Mantgem et al. 2009; Williams et al. 2010), the response of forest structure, composition, growth, and vitality at spatiotemporal scales requires thorough examination (Babst et al. 2018).

Climate change is likely to have significant impacts on the structure and function of California's

---

Supported by the Hispanic-Serving Institution's Education Grants Program, Grant No. 2015-38422-24058/project accession No. 1007104, from the USDA National Institute of Food and Agriculture.

ecosystems (Allen et al. 2010; Dolanc et al. 2013a; Jones 2015; Schladow 2018; Vose et al. 2018). These fluctuations in climate are accompanied by detectable trends in many ecological processes and species dynamics such as an increase in wildfire activity (Allen et al. 2010), changes in plant phenology (Vose et al. 2018), warming-induced increases in tree mortality rates (Van Mantgem et al. 2009), and elevational shifts in species distributions (Millar et al. 2004; Bunn et al. 2005). Previous studies have reported considerable changes in the forest ecosystem in the Sierra Nevada in recent decades. Regional analysis by Van Mantgem et al. (2009) revealed a slight decline in density and basal area but increased mortality due to warming in the region. Whereas, the same warming favoured increased growth at the upper forest limit (Bunn et al. 2005). Dolanc et al. (2013a, 2014) evidenced increasingly densifying stands (more small trees, few large trees) with low mortality in Yosemite National Park. But, increased basal area and decreased tree number are the recent findings from the Jeffery pine (*Pinus jeffreyi* Grev. & Balf.) forest in the Lake Tahoe Basin (Taylor et al. 2014). Severe drought and accompanying insect outbreaks were pronounced events recently observed in California. The five-year prolonged drought (2011–2016) led to the mortality of over 129 million trees in California (Vose et al. 2018). Even with the years 2016 and 2017 that received enough precipitation, due to the stress and drought legacy as well as insect infestations, trees continued dying. Such events thus can rapidly alter forest dynamics and structure (Dolanc et al. 2014).

Vegetation models incorporating mechanistic relationships of plant physiology, climate, and fire regimes have predicted a substantial decline in major vegetation types in California (Dolanc et al. 2013a). However, there exist stand level and species-specific responses to warming and interactions of various disturbance factors. Increased urgency is in current unprecedented and predicted climate change scenarios, the fine-scale understandings (local and species level) of tree responses (Williams et al. 2010). Since tree-rings embed climatic signals, tree-ring based studies (dendrochronology) facilitate the understandings of retrospective forest ecosystem dynamics in relation to climatic forcing (Fritts 1976), the knowledge, inevitable in assessing and anticipating forest responses to future climatic conditions (Williams et al. 2010). Tree-rings belong to several natural sources of information on the past climate conditions of a geographic area with their strengths in archiving long-term climate signals in annual resolution (Williams et al. 2010) and synchronous inter-annual variability at a regional scale. However, different non-climatic, biotic, and abiotic environmental drivers, tree's physiological state, and their interactions modulate the response to regional climatic forcing (Fritts 1976) that are archived at very local and variable tree-ring patterns and structures (Rathgeber et al. 2016). Therefore, more studies at a local scale (micro-catchment level) provide greater detail and an accurate depiction of current and possible future species response to regional/global climate variability (Dolanc et al. 2013b).

Few studies have been carried out in the Lake Tahoe Basin to understand tree growth and climate response (Dolanc et al. 2013a; Taylor et al. 2014) with some site and species-specific discrepancies. Even fewer studies have compared ring width index (RWI) and basal area increment (BAI) in radial growth trend analysis considering recent atmospheric warming as well as a marked rise in the Lake Tahoe surface water (Schladow 2018) and recent prolonged severe drought event (Vose et al. 2018; Lepley et al. 2020). It is essential to know how a particular tree species in the Lake Tahoe Basin is responding to the changes. In these scenarios, our objectives were to (*i*) develop a tree-ring chronology of Jeffrey pine to understand the historical radial growth trend, (*ii*) observe the basal area increment trend, and (*iii*) see the relationship between the growth and climate variables, identifying the principal climatic factors which limit tree growth.

MATERIAL AND METHODS

Study area. The Lake Tahoe Basin lies in the North Central Sierra Nevada, within California and Nevada. We collected tree-ring cores from Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) dominated subalpine forest at the elevation belt of 2 098–2 139 m a.s.l. around the Cascade Creek watershed. The area lies south to Lake Tahoe in the valley between Mt. Tallac and Maggie's Peak (Figure 1). Igneous intrusive (granodiorite in general) and igneous extrusive (typically andesitic lahar) rocks as well as some metamorphic rocks dominate the geology of the region (Maloney et al. 2016) with thin soil (Fites-Kaufman et al. 2007; Dolanc et al. 2013a, b). Jeffrey pine is usually found on drier sites, shallow

https://doi.org/10.17221/191/2020-JFS

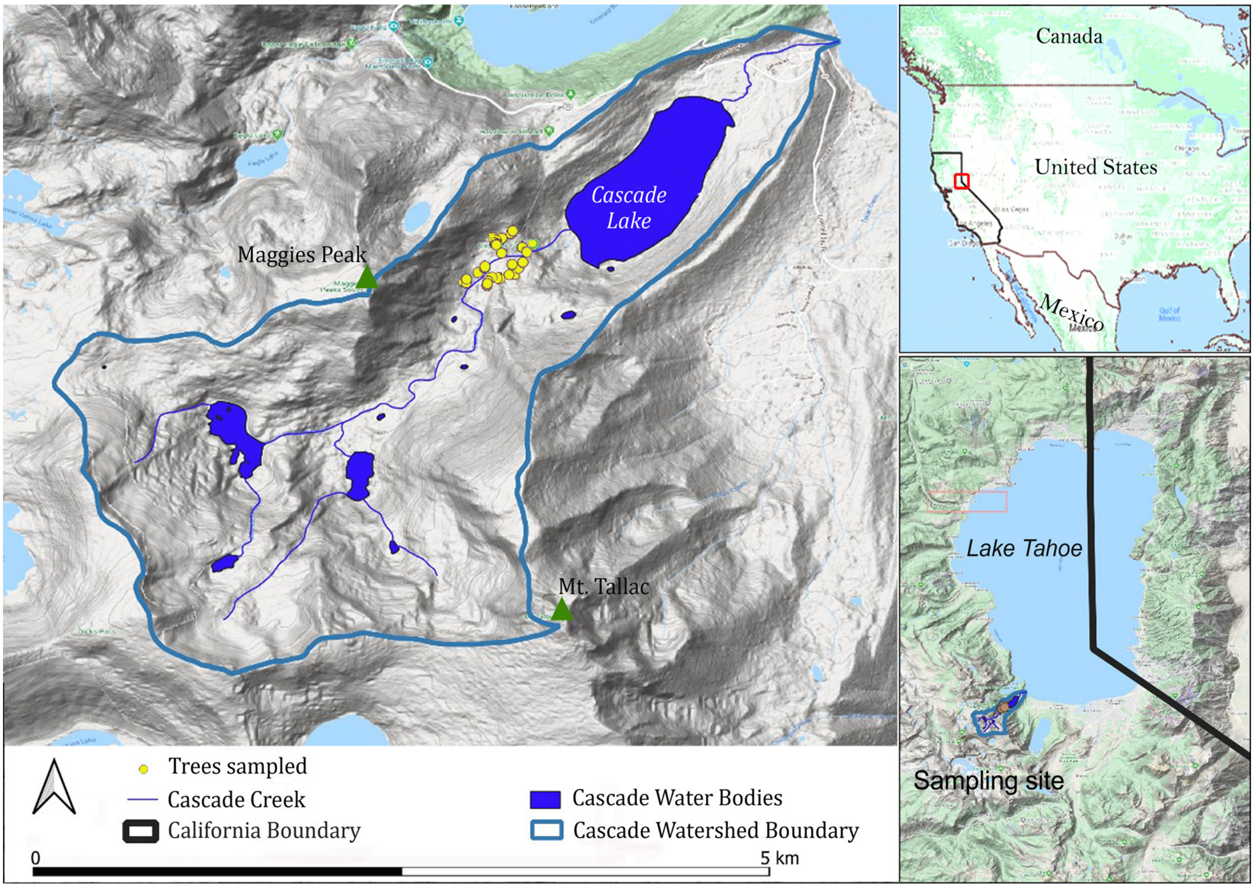

Figure 1. Location of sampling site within the Cascade Creek Watershed in the Lake Tahoe Basin, California; insets on the right show the location on a regional and local scale

soil, and typically in a relatively pure stand on the eastern slope in the Sierra Nevada and south of the Lake Tahoe Basin (Fites-Kaufman et al. 2007; Dolanc et al. 2013a), whereas it occurs mixed with white fir and incense cedar in western flanks at a lower elevation and with red fir and lodgepole pine at a higher elevation (Fites-Kaufman et al. 2007). Jeffrey pine primarily occurs in 1 500 to 1 800 m elevation belt in the northern Sierra Nevada and between 1 600 to 2 600 m in the southern Sierra Nevada (Fites-Kaufman et al. 2007) and it is the dominant species at lower elevations of the Lake Tahoe Basin around 2 000 m above which it starts occurring commonly associated with white fir (Taylor et al. 2014).

The Mediterranean-influenced climate of the study area is characterized by warm dry summer and cold wet winter. Nearly all the precipitation falls as snow between October and May, and a short dry growing season lasts 6–9 weeks (Fites-Kaufman et al. 2007; Maloney et al. 2016). The mean monthly air temperature ranges from –1.8 °C (January) to 16.3 °C (July), total annual precipitation is 800.5 mm [recorded at Tahoe City (1 898.9 m) meteorological station which is at about 10 km southeast from the sampling site]. The annual average temperature is 6.26 °C. The majority of all recorded precipitation occurs in the winter months mostly in the form of snowfall and the vegetation growth depends on precipitation and snowpack from the previous winter season (Peterson et al. 1990). December (140.3 mm), January (153.1 mm), and February (132.8 mm) are wet months, whereas July (6.5 mm) and August (7.6 mm) are the driest months. The annual trend of air temperature and precipitation has shown an increasing trend in recent decades (Figure 2).

Sample procedures and chronology development. In June 2019, we collected 44 tree-ring cores at random from 26 Jeffrey pine trees located around the Cascade lake watershed. Two cores per tree were collected along the contour line, away

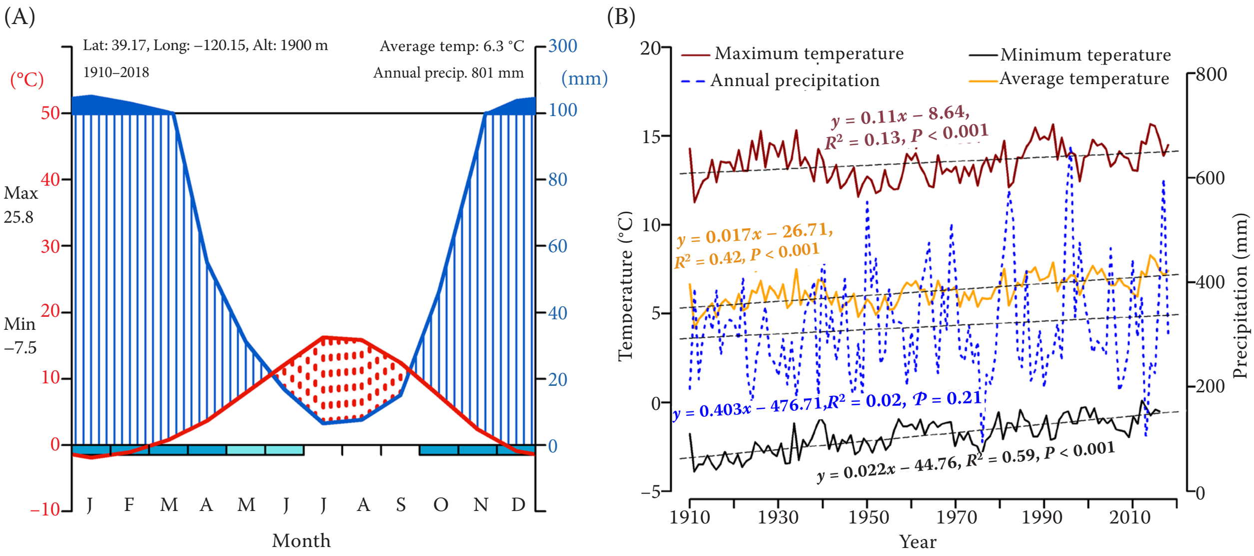

Figure 2. Monthly (A) and annual (B) climate of Tahoe city (closest to the study site); left y-axis (A) – temperature; right y-axis (A) – precipitation

from stream and water bodies. However, tree-ring cores from another side of some trees could not be extracted. Moreover, some trees had crumbled cores from the other side. Height, diameter at breast height (DBH), and canopy diameter of trees were also measured (Table 1). We placed cores in plastic straw pipes with proper labelling followed by a week-long period of air drying. Tree-ring cores were processed by the standard dendrochronological method to enhance the visibility of the tree-rings (Speer 2010). After getting well-surfaced cores with clear visualization of tracheid cells and ring boundaries, cores were dated visually and crossdated (Speer 2010). Then, tree-ring widths of all cores were carefully measured with the Velmex tree-ring measurement system (0.001 mm precision; Velmex, Inc., USA) fitted with MeasureJ2X measurement software (MeasureJ2X Version: 5.02, Year: 2017; VoorTech Consulting, USA), to create time series of ring widths for all cores. Measurement errors and accuracy of crossdating were statistically verified using COFECHA software (Holmes 1983; Cook, Kairiukstis 1990), which eased estimating missing rings or false rings in a core.

Table 1. Sampling site characteristics and sampled trees

Variables	Value
Elevation range (m a.s.l)	2 098–2 139
Aspect	east
Average slope (degree)	20
Average tree DBH (cm)	206
Average tree height (m)	23
Average tree canopy (m)	11
Average age of trees sampled (years)	173
No. of trees (cores)	26 (44)

DBH – diameter at breast height

All crossdated ring-width series were standardized to remove the age-related trend to strengthen climate signals (Cook, Kairiukstis 1990). Each tree-ring series was detrended with a spline of a 50% frequency response at a wavelength of 30 years rigidity, and then the standard chronology or ring-width index (RWI) chronology – which is a biweight robust mean of all detrended index series – was developed using dplR (Bunn 2008) in R statistical program (Version 4.0.2, 2020). We checked chronology quality by using R-bar and Expressed Population Signal (EPS) statistics (Wigley et al. 1984; Briffa 1999). We discarded thirteen problematic cores such as crumbled ones, cores with an unusually higher number of missing rings, cores containing reaction wood, and unusual scars because such types of unexpected cores might be affected more by non-climatic factors and might not be reliable in growth climate analysis.

We analysed the pointer years through relative growth change (Schweingruber et al. 1990) to see remarkable changes in tree rings. In defining event years, we compared the relative ring width change of the year (at least 10% wider or narrower) with

https://doi.org/10.17221/191/2020-JFS

the average of the ring width of the previous four years and with the change in at least 75% of the 31 series (Lebourgeois 2000). The analysis was performed using the pointRes package (van der Maaten-Theunissen et al. 2015) in R statistical program. The pointer year analysis provided important clues in crossdating as well. Moreover, the ring width series were transformed into basal area increment series using dplR (Bunn 2008), quantifying the amount of biomass a tree would have accumulated each year in the forest stand.

Tree-ring and climate response. We carried out a correlation (Pearson's correlation coefficient) between RWI and monthly climate data from Tahoe City, using the 'treeclim' package (Zang, Biondi 2015) in R program. This allowed us to examine the statistical relationship between RWI and annual air temperature and precipitation trends. We also ran a correlation analysis between the RWI and Palmer Drought Severity Index (PDSI), which is a drought index used to assess the severity of dry or wet spells of weather. PDSI integrates air temperature and precipitation and is calculated in a way that is cumulative over time (Dolanc et al. 2013b). PDSI is useful in understanding forest response because it has more biological meaning than precipitation in interpretations of tree growth response to climate conditions (Lebourgeois et al. 2005; Rathgeber et al. 2005). According to Palmer (1965), PDSI values between 0.5 and –0.5 are near normal. Dry spells are such that their values –0.5 to –1.0 are classified as incipient drought; –1.0 to –2.0 as mild drought; –2.0 to –3.0 as moderate drought; –3.0 to –4.0 as severe drought; and greater than –4.0 as extreme drought. Wet spells are also classified using similar adjectives for the respective positive value ranges. The monthly PDSI data (1895–2019) were obtained from the National Environmental Satellite, Data, and Information Service (NESDIS 2020) of the National Oceanic and Atmospheric Administration (NOAA); National Climatic Data Center, Divisional Data for CA-2, Sacramento Drainage. We analysed the correlation within the 18-month window (from previous May to the current year October) for the common period of 1910–2017.

RESULTS

Tree-ring chronology and growth pattern. A 370-year chronology spanning from 1648–2018 was constructed from the sample set, containing 31 cores from 21 trees (Figure 3). The mean value of the expressed population signal (EPS) for the entire chronology was 0.88. The EPS threshold value above 0.85 suggests a strong climate signal in the chronology, and the sample size in our study was sufficient to represent the population (Wigley et al. 1984). The EPS threshold value was achieved after 1775 with at least ten series afterward. Therefore, the EPS of the chronology subsample with an acceptable level of chronology confidence was 0.96. The mean sensitivity of 0.25 indicated considerable inter-annual growth variation which means changes in local environmental conditions have consid-

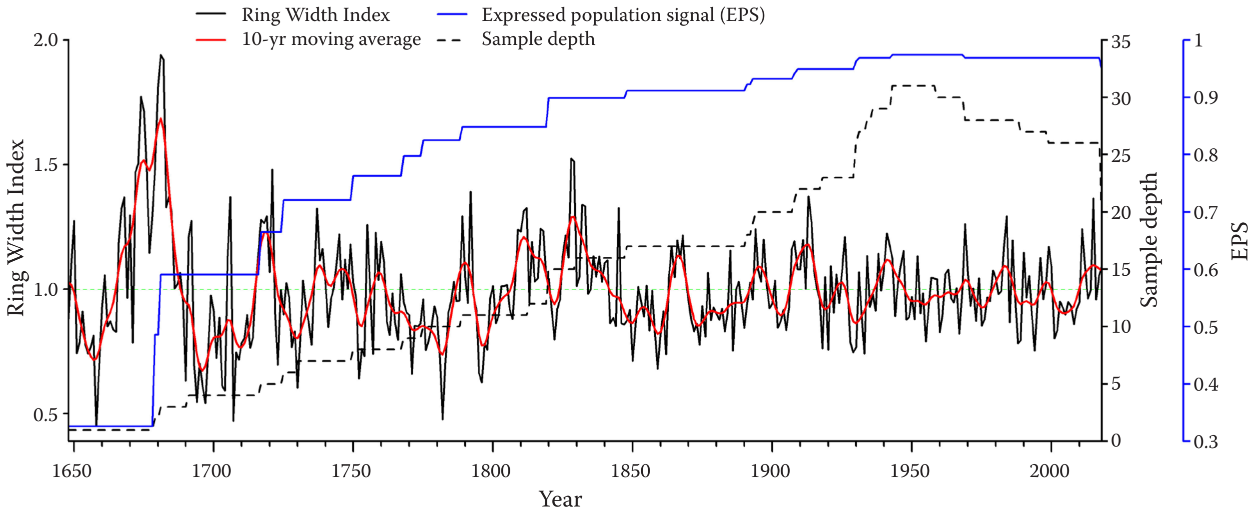

Figure 3. Ring width index chronology of Jeffery pine showing years of robust and narrow growth with a trend line indicating a decadal moving average

erable influences on growth. Furthermore, the high value of the first-order autocorrelation coefficient (0.61) implies a significant influence of current year growth conditions on the tree growth in the following year. A mean correlation of 0.49 with master chronology suggested a good common signal of tree growth to climatic variables. Thus, Jeffrey pine appeared to have a dendrochronological potential, and the chronology we prepared can be used for further analysis. Some of the statistics of the standard chronology are shown in Table 2.

Table 2. Chronology statistics of Jeffery pine

Variables	Value
No. of trees (cores)	21 (31)
Average series length (years)	179.96
Chronology length	370 (1648–2018)
Mean ring width (mm)	1.51 (SD = 0.63)
Mean sensitivity (MS)	0.25
RWI standard deviation (SD)	0.40
Mean correlation of raw series (with master chronology)	0.49
Mean inter-series correlation (Rbar)	0.27
Auto correlation (AR1)	0.62
Signal-to-noise ratio (SNR)	5.58
Expressed population signal (EPS)	0.88
Subsample strength (EPS > 0.85) start year (minimum sample depth)	1 775 (10)

The standard chronology (RWI) showed a growth variation (Figure 3) with an obvious growth increase from the late 1990s. The years 1707, 1723, 1757, 1782, 1886, 1859, 1876, 1918, 1920, 1928–30, 1933, 1977, 1988–89, 1994–95, 2001–02, 2008, 2014, 2016 exhibited low growth (narrow rings) and the years 1747, 1749, 1792, 1828, 1866, 1868, 1907–08, 1913–14, 1940–43, 1969, 1983–84, 1998–2000, 2011 and even 2015 exhibited robust growth (wider rings). Missing rings were rare in 31 tree cores we used, indicating the absence of fatal adversity endured by Jeffrey pine. One core each for 2012 and 2013 had locally absent rings. A recent period (from the 2000s) of a slightly increasing trend of ring width was observed in 10 years moving average of RWI (Figure 3). Moreover, the transformation of ring width series to BAI series (Figure 4) clearly showed an increasing growth trend, with some distinct growth rate depression in 1920 to mid-1930s, 1988–89, and 2001–02. The ring width chronology (Figure 4) showed an almost constant growth trend which usually would be negative exponential, typical of growing and aging stands. Thus, RWI chronology however somewhat has masked the growth trend in the forest stand. BAI thereby clearly showed overall productivity trends in the forest stand.

Relative growth changes were found as negative or positive pointer years (Figure 5). For example, the years 1786, 1799, 1800, 1828, 1845, 1875, 1907–08, 1934, 1968, 1984, 1996, and 2011 were years of somewhat abrupt growth. Likewise, the years 1721–22, 1752, 1782, 1795–96, 1820–22, 1842, 1859, 1944, 1973, 1985, 1988, 1994, and 2001 were few examples of negative growth years. The frequency of low growth episodes was higher in the 18th century than in later periods. These patterns in the 20th century

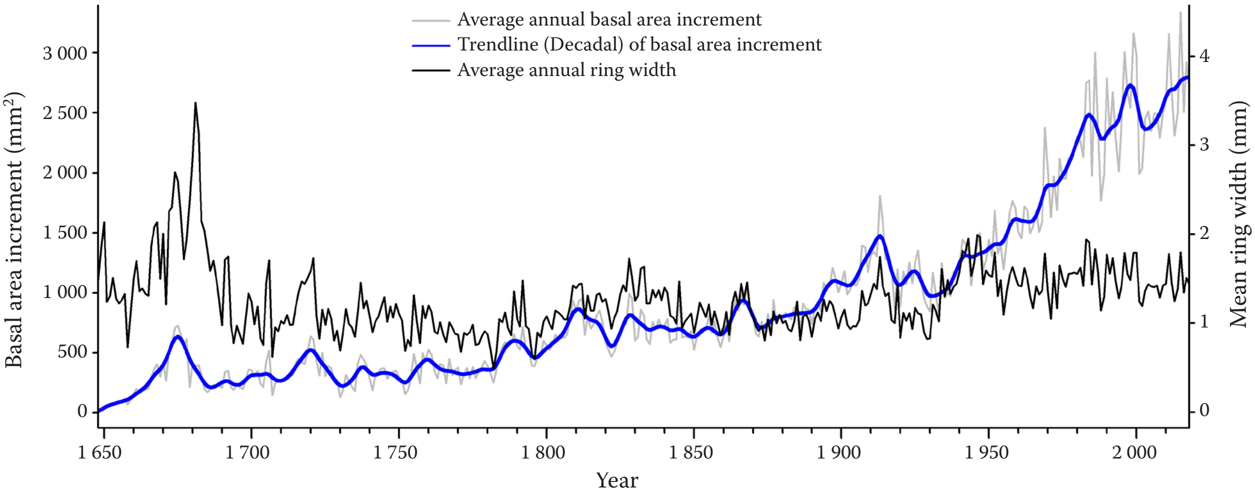

Figure 4. Annual basal area increment (BAI) rate

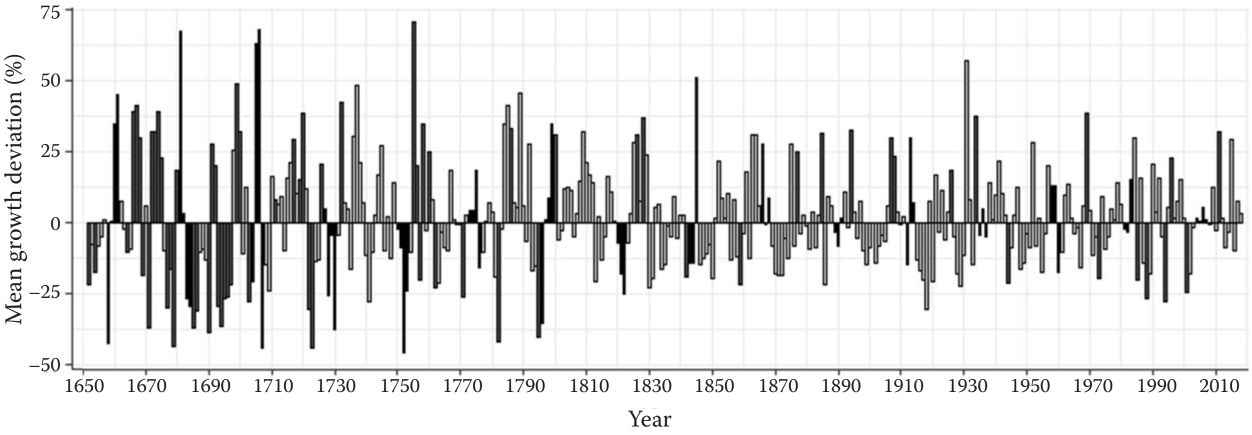

Figure 5. Pointer years (relative growth change) in Jeffery pine chronology (1648–2018)

were in agreement with the PDSI index of the region, especially for positive values. For example, the periods of 1906–08, 1957–58, 1967–70, 1983, 1996, 2010–11 were of positive PDSI year, positive pointer years, and so has been shown by BAI rate as well. While dry conditions characterize the forest site, as depicted by the PDSI values, the trees showed negative growth changes in more intense droughts. This includes the years 1943, 1959–61, 1972, 1984–85, 1987–88, 1994, 1999–2002, where episodes of intense drought coincided with the negative relative growth during or following the drought years. After 2001, irrespective of the drought spell in California, especially between 2011 and 2017 (NIDIS 2020), there were not any negative pointer years in recent years despite drought between 2012 and 2015 and in winter of 2017 and 2018 (NESDIS 2020). However, the RWI and BAI chronologies showed a slight decline in overall growth rate during 2013–2014 (2013 being the driest year in instrumental record, with 89.9 mm annual precipitation) and 2016. On the surface, the pointer year analysis and BAI indicated that the Cascade creek watershed was not affected much by the recent prolonged drought episode.

Tree-ring and climate response. The climate-growth response analysis showed varied correlations over time. The radial growth was found to have a significant positive correlation with precipitation in previous year's May ($r = 0.19$, $P < 0.05$), August ($r = 0.21$, $P < 0.05$), and September ($r = 0.24$, $P < 0.01$). Likewise, the current year's February ($r = 0.29$, $P < 0.01$) and July ($r = 0.25$, $P < 0.01$) precipitation also had a significant positive influence on tree growth (Figure 6). Seasonal influence of

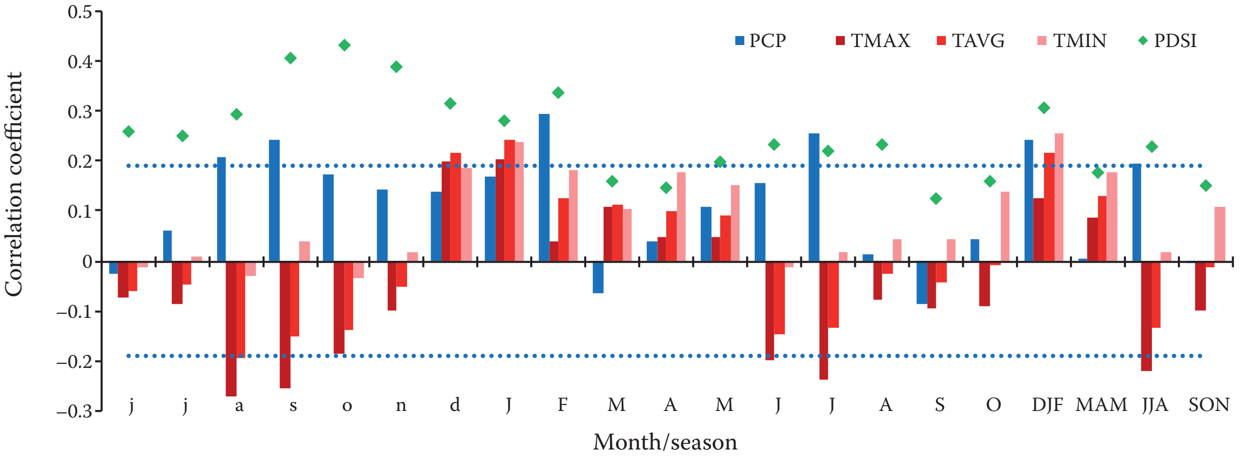

Figure 6. Growth response correlation with precipitation (blue bar), maximum temperature (dark red bar), mean temperature (red bar), minimum temperature (pink bar), and PDSI (◆) from the common period 1910–2017

Small letters on the x-axis – months of previous year; capital letters – the current year months; DJF – winter season; MAM – spring season; JJA – summer season; SON – autumn season; horizontal blue dashed lines – the correlation significant at 95% confidence levels

https://doi.org/10.17221/191/2020-JFS

winter ($r = 0.24$, $P < 0.05$) and summer precipitation ($r = 0.19$, $P < 0.05$) was particularly evident.

By contrast, we observed an inverse relationship with air temperature, particularly summer maximum temperature ($r = -0.22$, $P < 0.05$). Previous year's May ($r = -0.24$, $P < 0.05$), August ($r = -0.28$, $P < 0.01$), and September ($r = -0.26$, $P < 0.01$) were found to have a significant negative impact on growth. In addition, higher temperatures of the current year June ($r = -0.20$, $P < 0.05$) and July ($r = -0.24$, $P < 0.05$) were also found to be unfavourable to growth. The winter months, previous year's December ($r = -0.20$, $P < 0.05$) and current year's January ($r = -0.20$, $P < 0.05$) temperatures, however, were found to be positively correlated with the radial growth (Figure 6). Compared to maximum temperature, the average and minimum temperature had lower importance in tree growth (Figure 6), however, the reverse was true of winter when higher winter minimum temperature had a higher influence on radial growth.

The tree-ring chronology showed a strong correlation of growth with PDSI. March and April of the growing season and September, October, November, and December, previous year's summer and winter months as well as current year's summer month PDSI were found to have a positive correlation with growth at a 95% confidence level. The previous year's PDSI was found to be more meaningful.

DISCUSSION

The results highlighted a growth increase of the Jeffrey pine stand in the Cascade creek watershed, despite recent developments in regional climatic patterns which have been increasingly unfavourable for forest productivity. We found the seasonal importance of temperature and precipitation in the growth dynamics. The Mediterranean characteristic summer drought has been found to limit the tree growth (Peterson 1998; Dolanc et al. 2013b), but, more than the current year climate, the conditions prior to the growing season have more relative importance. The soil water balance has more biological meaning in explaining tree growth response to climate conditions (Rathgeber et al. 2005). The importance of soil water availability has been underlined by the positive correlation of RWI with PDSI, more significantly with drought indices for months prior to the growing season.

Tree-ring chronology and growth patterns. The chronology statistic of the Jeffery pine in this study is comparable with previous studies from the region (Dolanc et al. 2013b) with similar signal strength and 20th-century growth patterns. Low growth years observed in Jeffery pine RWI and BAI chronologies coincide with historical drought events in California (Jones 2015). Based on this strong correlation we have inferred some likely drought-stressed years in the last three centuries. The higher frequency of low growth events in the 18th century than that in the 19th and 20th centuries closely matches other reconstructed drought events in California (Meko, Woodhouse 2005; Griffin, Anchukaitis 2014). Incorporating more species from the study area will help better understand the nature and coherence of past drought events and help predict the directionality of response to possible future drought occurrences.

BAI indicated some low growth periods associated with extreme drought events, not well detected in RWI and pointer year analysis. The RWI showed growth variation over time, but an obvious increasing growth trend in recent decades picked by BAI chronology indicated its usefulness in understanding forest productivity trends over time (Peterson et al. 1990). For a healthy forest stand, BAI provides a biologically meaningful variable showing growth trends independently of tree age (Biondi, Qeadan 2008; Marqués et al. 2016; Marziliano et al. 2019). Several studies (LeBlanc 1990; Zhang et al. 2020) have also indicated that BAI is better for accessing tree radial growth because BAI minimizes the age-related growth trend (Weiner, Thomas 2001) in assessing productivity. A conifer growth increase, especially after the latter half of the 20th century in the Sierra Nevada, has been evident in some other studies from the region. Whitebark pine and lodgepole pine in the Eastern Brook Lake area have shown increased BAI at all ages and the trend has been sharp since the 1970s, most likely because of stand dynamic effects and climatic favourability (Peterson et al. 1990). Bunn et al. (2005) and Salzer et al. (2009) also reported recent increases in the growth of different pine species, more pronouncedly at a higher elevation in White Mountain. Dolanc et al. (2013a) found more than 30% increase in tree density in the subalpine forest in the Central Sierra Nevada, mainly due to warming and increased precipitation. Depressions in Jeffrey pine BAI chronology and major drought episodes in the

1920s and early 1930s, 1987–89, 2001–02 coincide. Barring this period, the BAI trend did not show any major depressions over time, and thus the BAI can be assumed to explain climatic controls on forest growth. We are unclear about the site history of our site. Therefore, likely explanations for the growth increment may be the warmer and longer growing season (Millar et al. 2004; Dolanc et al. 2013a) or logging and long absence of fire (Fites-Kaufman et al. 2007; Dolanc et al. 2013a, 2014; Taylor et al. 2014). We cannot neglect carbon dioxide fertilization, as this phenomenon was speculated to cause the increased BAI of *Juniperus thurifera* in Central Spain (Granda et al. 2013).

Tree-ring and climate response. Previous studies have shown a positive influence on tree growth from higher precipitation and warmer temperature prior to and during the growing season (Peterson et al. 1990; Dolanc et al. 2013b). Our analysis also found moisture and temperature significantly influencing tree growth. Late summer drought dominates the growing season in the Sierra Nevada (Dolanc et al. 2014). The positive correlation with precipitation coupled with a negative correlation with temperature during summer reflects the drought stress impact on the summer growth pattern. This finding is similar to the previously carried out studies from the region (Ettl, Peterson 1995; Peterson et al. 2002). Peterson et al. (2002) also observed on the driest and warmest sites of Pacific Northwest that tree growth was negatively correlated with previous summer temperature, suggesting that low summer soil moisture limits growth. Ettl and Peterson (1995) also recorded *Abies lasiocarpa* (subalpine fir) from the Olympic mountains in Washington negatively correlated with the previous year August temperature and positively with summer precipitation, indicating the impact of high temperature and low soil moisture on tree growth in subsequent years. Granda et al. (2013) also found in their study in Central Spain that *Juniperus thurifera* and *Pinus nigra* responded to climatic variables in a similar way. In the Mediterranean habitat, growing season precipitation had a positive influence on growth. Furthermore, the significance of previous year's autumn precipitation highlighted the temporal autocorrelation.

Climatic parameters have differential temporal importance. Precipitation and temperature combination during winter months was shown conducive to growth. However, no such a significant influence was evident even during the spring season. While temperature and precipitation of the current year growing season did not have a substantial influence, the previous year's late spring temperature showed a negative correlation with growth, similar to the response of Jeffrey pine stands in a study by Dolanc et al. (2013b). Temperature, precipitation, and evapotranspiration modulate the soil moisture that has been found to be strongly correlated with tree growth (Leblanc, Terrell 2001) because the soil water balance during the growing season is particularly essential for plant metabolic, physiological, and growth processes (Leblanc, Terrell 2001; Rathgeber et al. 2005; Granier et al. 2007). Thus, the correlation analysis suggested that rather than the current year growing season climate, previous year's cool and moist summer, and warmer wet winter preceding the growing season are growth driving climate factors.

Warming and reduced precipitation have been increasingly limiting tree growth in the Mediterranean regions (Lebourgeois et al. 2005; Granier et al. 2007; Proutsos, Tigkas 2020). Drought has legacy effects weakening tree's resilience for a few years after drought episode (Granda et al. 2013; Proutsos, Tigkas 2020). However, the time lag effects can be counterbalanced by recovery capacity (Granda et al. 2013). Jeffrey pine showing a higher autocorrelation appears to store carbohydrates to be used for the subsequent year, and the resilience might have countered the drought legacy. Therefore, even during or after the recent extreme drought years (1976 and 2013), no sharp growth decline was observed as expected. Though, with anticipated frequent and intense drought conditions in future, a decline in the recovery capacity is more likely in Mediterranean species (Allen et al. 2010, Granda et al. 2013).

In line with the findings of Dolanc et al. (2013b), a noticeable response is that radial growth was found to be correlated more with PDSI (that of the previous year is even more important), and the relation was more prevailing compared to temperature and precipitation indicating the importance of water balance rather than meteorological numbers of temperature and precipitation (Rathgeber et al. 2005). While there appeared the prolonged air drought when California faced the longest historical drought from 2011 to 2016 (Griffin, Anchukaitis 2014; NIDIS 2020), PDSI and many frequent low growth years observed in our analysis show that the intensity and duration of drought events were not uncommon in the past. In terms of precipitation anomalies, there were frequent similar or more severe deficits as the latest drought episodes in California in the past few centuries (Griffin, Anchukaitis 2014), but, the recent deficits were severely exacerbated by high temperature. However, contrary to what we had expected, tree growth was unlikely limited during the elsewhere adverse period, as shown in Figures 3 and 4. Figure 6 clearly shows that the growing season constraints in terms of soil water availability for Jeffrey pine were not pronouncedly limiting. A weaker growth correlation with temperature, precipitation, and PDSI during spring and a rather higher and significant correlation with summer and winter suggest that climatic conditions during these two seasons, particularly preceding the growing season, are more important in pine growth.

Trees in limiting soil water conditions have been found to respond more sensitively to climatic variations than those from favourable conditions (Fritts 1976; Lebourgeois et al. 2005). Characteristics of drought tolerance, cold hardiness, and adaptation to the short growing season allow Jeffrey pine thriving in stressful environments such as dry sites, ridge tops with shallow soil (Hubbert et al. 2001; Fites-Kaufman et al. 2007) where a deep root system is most likely the survival strategy. The significant proportion of snowfall in the total precipitation may be a possible reason behind the low correlation between PDSI and the growth in current year spring and summer. PDSI incorporates precipitation and temperature to indicate soil moisture (Dai et al. 2004; Dolanc et al. 2013b). However, because it treats all forms of precipitation as immediate rainfall, the use of PDSI as an indicator of soil moisture – for a region with a higher proportion of snowfall that accumulates for later melting tends to be imprecise (Dai et al. 2004). Therefore, in the high altitude areas like our study site where there is significant snowpack that melts until late spring, the PDSI may not reflect precisely the soil moisture. From the global dataset, Dai et al. (2004) reported a strong correlation between the PDSI variations and the soil moisture within one-meter soil depth in warmer months, the correlation being stronger in the late summer and weakest in the spring. The deep root system may allow Jeffrey pine to be unaffected much by low moisture in topsoil, which is reflected by PDSI. Deep snowpack during the spring and the subsequent melting may recharge the deep soil that Jeffrey pine benefits from. Because deeper soil moisture is available for the species, current year spring and summer PDSI reflecting just topsoil moisture appears to be less important than the prior spring precipitation that contributes to the deep soil moisture. In a high elevation stand from Mt. Etna in Italy, the correlation between PDSI and ring width revealed the moisture not limiting tree growth strongly (Seiler et al. 2017). The low influence was attributed to the snowy high elevation and proximity to the Mediterranean Sea, more specifically the snowmelt coming from spring precipitation utilized during summer droughts. Similar precipitation patterns seem to result in a low growth correlation with current spring PDSI. However, the Jeffrey pine growth sensitivity to PDSI of months before spring may imply that any change conducive to moisture disruption poses a threat to the individual trees in subsequent years. However, in the current scenario, warming and lengthened spring most likely could favour growth. Although the recent drought episodes affected Jeffrey pine forests on the western slope in the Lake Tahoe Basin (Vose et al. 2018), our analysis showed an insignificant impact on the eastern slope in the Cascade creek watershed. With all these response factors considered, extensive studies are yet to be carried out to determine the response of native California tree species to ongoing climate variability.

CONCLUSION

The negative growth correlation with summer temperature and positive correlation with precipitation means Jeffery pine has an adverse reaction to drought events, which are frequent in California. Warm and wet winter though was found to favour tree growth. The strong radial growth correlation with PDSI suggested the drought sensitivity of Jeffrey pine. However, BAI has shown an increasing growth trend in recent decades. While warming wet winter and possibly the lengthening growing season appeared to stimulate tree growth, the positive impact of spring temperature is less likely to reverse the influence on tree growth any soon. Only in the future when the change in climate renders the growing season devoid of snow, the increased temperature then may bring a possible growth reduction. Only the summer drought apparently has growth control at present. Generally, subalpine conifers are stress-tolerant, and mature trees can endure an environmental change to some extent (Dolanc et al. 2013a). Climate change thus likely causes long-term and lagged changes. Meanwhile, since we analyzed on the basis of core samples mostly from mature trees, we cannot generalize the growth response of climate-sensitive younger individuals. Moreover, because increased environment stress and changes in physiological responses of trees can reduce the climate sensitivity of trees (Jiao et al. 2015), such divergent problems need to be analyzed. Therefore, close scrutiny of disturbance factors, forest structure, composition, thorough examination of growth cyclicity as well as intra-seasonal influences of climate variables on plants' growth habits in growing and non-growing season, incorporating ecophysiological and wood anatomical studies, and integrating other species from the region would better aid in climate reconstruction and forest growth dynamics.

Acknowledgement: We acknowledge the "McNair Scholars Program", and "CSUDH Research, Scholarship, and Creative Activity (RSCA) award program".

REFERENCES

Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D.D., Hogg E.H., Gonzalez P., Fensham R., Zhang Z., Castro J., Demidova N., Lim J.-H., Allard G., Running S.W., Semerci A., Cobb N. (2010): A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, 259: 660–684.

Babst F., Bodesheim P., Charney N., Friend A.D., Girardin M.P., Klesse S., Moore D.J.P., Seftigen K., Björklund J., Bouriaud O., Dawson A., DeRose R.J., Dietze M.C., Eckes A.H., Enquist B., Frank D.C., Mahecha M.D., Poulter B., Record S., Trouet V., Turton R.H., Zhang Z., Evans M.E.K. (2018): When tree rings go global: Challenges and opportunities for retro- and prospective insight. Quaternary Science Reviews, 197: 1–20.

Biondi F., Qeadan F. (2008): A theory-driven approach to tree-ring standardization: Defining the biological trend from expected basal area increment. Tree-Ring Research, 64: 81–96.

Briffa K.R. (1999): Interpreting high-resolution proxy climate data – the example of dendroclimatology. In: von Storch H., Navarra A. (eds): Analysis of Climate Variability. Berlin, Springer: 77–94.

Bunn A.G. (2008): A dendrochronology program library in R (dplR). Dendrochronologia, 26: 115–124.

Bunn A.G., Graumlich L.J., Urban D.L. (2005): Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. The Holocene, 15: 481–488.

Cook E.R., Kairiukstis L.A. (1990): Methods of Dendrochronology: Applications in the Environmental Science. Dordrecht, Kluwer Academic Publishers: 394.

Dai A., Trenberth K.E., Qian T. (2004): A global dataset of Palmer Drought Severity Index for 1870–2002: Relationship with soil moisture and effects of surface warming. Journal of Hydrometeorology, 5: 1117–1130.

Dolanc C.R., Thorne J.H., Safford H.D. (2013a): Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. Global Ecology and Biogeography, 22: 264–276.

Dolanc C.R., Westfall R.D., Safford H.D., Thorne J.H., Schwartz M.W. (2013b): Growth-climate relationships for six subalpine tree species in a Mediterranean climate. Canadian Journal of Forest Research, 43: 1114–1126.

Dolanc C.R., Safford H.D., Thorne J.H., Dobrowski S.Z. (2014): Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s. Ecosphere, 5: 1–26.

Ettl G.J., Peterson D.L. (1995): Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. Global Change Biology, 1: 213–230.

Fites-Kaufman J.A., Rundel P., Stephenson N., Weixelman D.A. (2007): Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In: Barbour M., Keeler-Wolf T., Schoenherr A.A. (eds): Terrestrial Vegetation of California. 3rd Ed. Berkley, University of California Press: 456–501.

Fritts H.C. (1976): Tree Rings and Climate. London, Academic Press: 567.

Granda E., Camarero J.J., Gimeno T.E., Martinez-Fernandez J., Valladares F. (2013): Intensity and timing of warming and drought differentially affect growth patterns of co-occurring Mediterranean tree species. European Journal of Forest Research, 132: 469–480.

Granier A., Reichstein M., Bréda N., Janssens I.A., Falge E., Ciais P., Grünwald T., Aubinet M.,et al. (2007): Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agricultural and Forest Meteorology, 143: 123–145.

Griffin D., Anchukaitis K.J. (2014): How unusual is the 2012–2014 California drought? Geophysical Research Letters, 41: 9017–9023.

Holmes R.L. (1983): Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin, 43: 69–75.

Hubbert K.R., Graham R.C., Anderson M.A. (2001): Soil and weathered bedrock: Components of a Jeffrey pine plantation substrate. Soil Science Society of America Journal, 65: 1255–1262.

Jiao L., Jiang Y., Zhang W.-T., Wang M.-C., Zhang L.-N., Zhao S.-D. (2015): Divergent responses to climate factors in the radial growth of *Larix sibirica* in the eastern Tianshan Mountains, northwest China. Trees, 29: 1673–1686.

Jones J. (2015): California's most significant droughts: Comparing historical and recent conditions. California Department of Water Resources, State of California. Available at: https://cawaterlibrary.net/wp-content/uploads/2017/09/California_Signficant_Droughts_2015.pdf (accessed August 18, 2020).

LeBlanc D.C. (1990): Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Canadian Journal of Forest Research, 20: 1399–1407.

LeBlanc D., Terrell M. (2001): Dendroclimatic analyses using Thornthwaite-Mather-type evapotranspiration models: A bridge between dendroecology and forest simulation models. Tree-Ring Research, 57: 55–66.

Lebourgeois F. (2000): Climatic signals in earlywood, latewood and total ring width of Corsican pine from western France. Annals of Forest Science, 57: 155–164.

Lebourgeois F., Bréda N., Ulrich E., Granier A. (2005): Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). Trees, 19: 385–401.

Lepley K., Touchan R., Meko D., Shamir E., Graham R., Falk D. (2020): A multi-century Sierra Nevada snowpack reconstruction modeled using upper-elevation coniferous tree rings (California, USA). The Holocene, 30: 1266–1278.

Maloney P.E., Eckert A.J., Vogler D.R., Jensen C.E., Delfino Mix A., Neale D.B. (2016): Landscape biology of Western White Pine: Implications for conservation of a widely-distributed five-needle pine at its southern range limit. Forests, 7: 93.

Marqués L., Camarero J.J., Gazol A., Zavala M.A. (2016): Drought impacts on tree growth of two pine species along an altitudinal gradient and their use as early-warning signals of potential shifts in tree species distributions. Forest Ecology and Management, 381: 157–167.

Marziliano P.A., Tognetti R., Lombardi F. (2019): Is tree age or tree size reducing height increment in *Abies alba* Mill. at its southernmost distribution limit? Annals of Forest Science, 76: 17.

Meko D.M., Woodhouse C.A. (2005): Tree-ring footprint of joint hydrologic drought in Sacramento and Upper Colorado river basins, western USA. Journal of Hydrology, 308: 196–213.

Millar C.I., Westfall R.D., Delany D.L., King J.C., Graumlich L.J. (2004): Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. Arctic, Antarctic, and Alpine Research, 36: 181–200.

NIDIS (2020): What is NIDIS? National Integrated Drought Information System,| Drought.gov. Available at: https://www.drought.gov/drought/what-nidis

NESDIS (2020): Divisional Data Select. National Environmental Satellite, Data, and Information Service Available at: https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp

Palmer W.C. (1965): Meteorological Drought. Washington, U.S. Department of Commerce, Weather Bureau: 68.

Peterson D.L. (1998): Climate, limiting factors and environmental change in high-altitude forests of Western North America. In: Beniston M., Innes J.L. (eds): The Impacts of Climate Variability on Forests. Berlin, Heidelberg, Springer-Verlag: 191–208.

Peterson D.L., Arbaugh M.J., Robinson L.J., Derderian B.R. (1990): Growth trends of whitebark pine and lodgepole pine in a subalpine Sierra Nevada forest, California, USA. Arctic and Alpine Research, 22: 233–243.

Peterson D.W., Peterson D.L., Ettl G.J. (2002): Growth responses of subalpine fir to climatic variability in the Pacific Northwest. Canadian Journal of Forest Research, 32: 1503–1517.

Proutsos N., Tigkas D. (2020): Growth response of endemic black pine trees to meteorological variations and drought episodes in a Mediterranean region. Atmosphere, 11: 554.

R Core Team (2020): R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.r-project.org/

Rathgeber C.B.K., Misson L., Nicault A., Guiot J. (2005): Bioclimatic model of tree radial growth: Application to the French Mediterranean Aleppo pine forests. Trees, 19: 162–176.

Rathgeber C.B.K., Cuny H.E., Fonti P. (2016): Biological basis of tree-ring formation: A crash course. Frontiers in Plant Science, 7: 734.

Salzer M.W., Hughes M.K., Bunn A.G., Kipfmueller K.F. (2009): Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences, 106: 20348–20353.

Schladow S.G. (2018): Tahoe: State of the Lake Report. Available at: https://tahoe.ucdavis.edu/sites/g/files/dgvnsk4286/files/inline-files/SOTL_Complete_reduced_1.pdf

Schweingruber F.H., Eckstein D., Serre-Bachet F., Bräker O.U. (1990): Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia, 8: 9–38.

Seiler R., Kirchner J.W., Krusic P.J., Tognetti R., Houlie N., Andronico D., Cullotta S., Egli M., D'Arrigo R., Cherubini P. (2017): Insensitivity of tree-ring growth to temperature and precipitation sharpens the puzzle of enhanced pre-eruption NDVI on Mt. Etna (Italy). PLoS ONE, 12: e0169297.

Speer J.H. (2010): Fundamentals of Tree-ring Research. Tucson, University of Arizona Press: 333.

Taylor A.H., Vandervlugt A.M., Maxwell R.S., Beaty R.M., Airey C., Skinner C.N. (2014): Changes in forest structure, fuels and potential fire behaviour since 1873 in the Lake Tahoe Basin, USA. Applied Vegetation Science, 17: 17–31.

van der Maaten-Theunissen M., van der Maaten E., Bouriaud O. (2015): pointRes: An R package to analyze pointer years and components of resilience. Dendrochronologia, 35: 34–38.

Van Mantgem P.J., Stephenson N.L., Byrne J.C., Daniels L.D., Franklin J.F., Fulé P.Z., Harmon M.E., Larson A.J., Smith J.M., Taylor A.H., Veblen T.T. (2009): Widespread increase of tree mortality rates in the western United States. Science, 323: 521–524.

Vose J.M., Peterson D.L., Domke G.M., Fettig C.J., Joyce L.A., Keane R.E., Luce C.H., Prestemon J.P., Band L.E., et al. (eds) (2018): Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II. Washington DC, U.S. Global Change Research Program: 232–267.

Weiner J., Thomas S.C. (2001): The nature of tree growth and the "age-related decline in forest productivity". Oikos, 94: 374–376.

Wigley T.M.L., Briffa K.R., Jones P.D. (1984): On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. Journal of Climate and Applied Meteorology, 23: 201–213.

Williams A.P., Michaelsen J., Leavitt S.W., Still C.J. (2010): Using tree rings to predict the response of tree growth to climate change in the continental United States during the twenty-first century. Earth Interactions, 14: 1–20.

Zang C., Biondi F. (2015): treeclim: An R package for the numerical calibration of proxy-climate relationships. Ecography, 38: 431–436.

Zhang T., Huang L., Zhang R., Gao Y., Hu D., Yu S., Jiang S. (2020): The impacts of climatic factors on radial growth patterns at different stem heights in Schrenk spruce (*Picea schrenkiana*). Trees, 34: 163–175.

Received: November 6, 2020
Accepted: March 24, 2021