



Stronger influence of growth rate than severity of drought stress on mortality of large ponderosa pines during the 2012–2015 California drought

Rachel M. Keen¹ · Steve L. Voelker² · Barbara J. Bentz³ · S.-Y. Simon Wang⁴ · Ryan Ferrell⁵

Received: 28 April 2020 / Accepted: 25 September 2020 / Published online: 8 October 2020
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

Abstract

Forests in the western United States are being subject to more frequent and severe drought events as the climate warms. The 2012–2015 California drought is a recent example, whereby drought stress was exacerbated by a landscape-scale outbreak of western pine beetle (*Dendroctonus brevicomis*) and resulted in widespread mortality of dominant canopy species including ponderosa pine (*Pinus ponderosa*). In this study, we compared pairs of large surviving and beetle-killed ponderosa pines following the California drought in the southern Sierra Nevada to evaluate physiological characteristics related to survival. Inter-annual growth rates and tree-ring stable isotopes ($\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$) were utilized to compare severity of drought stress and climate sensitivity in ponderosa pines that survived and those that were killed by western pine beetle. Compared to beetle-killed trees, surviving trees had higher growth rates and grew in plots with lower ponderosa pine basal area. However, there were no detectable differences in tree-ring $\Delta^{13}\text{C}$, $\delta^{18}\text{O}$, or stable isotope sensitivity to drought-related meteorological variables. These results indicate that differences in severity of drought stress had little influence on local, inter-tree differences in growth rate and survival of large ponderosa pines during this drought event. Many previous studies have shown that large trees are more likely to be attacked and killed by bark beetles compared to small trees. Our results further suggest that among large ponderosa pines, those that were more resistant to drought stress and bark beetle attacks were in the upper echelon of growth rates among trees within a stand and across the landscape.

Keywords Drought · Climate change · Stable isotopes · Tree growth · Western pine beetle

Communicated by Jim Ehleringer.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-020-04771-0>) contains supplementary material, which is available to authorized users.

✉ Rachel M. Keen
rlease@ksu.edu

¹ Division of Biology, Kansas State University, Manhattan, KS, USA

² Department of Environmental and Forest Biology, SUNY ESF, Syracuse, NY, USA

³ USDA Forest Service, Rocky Mountain Research Station, Logan, UT, USA

⁴ Department of Plants, Soils and Climate, Utah State University, Logan, UT, USA

⁵ Pepperwood Preserve, Santa Rose, CA, USA

Introduction

Between 2010 and 2017, over 100 million trees died in California (CA) due to drought and bark beetle outbreaks. A large portion of this mortality (~96%) occurred during a severe drought event from 2012 to 2015 (hereafter referred to as the “CA Drought”) and these numbers were particularly severe for the central and southern portions of the Sierra Nevada (Moore et al. 2017; Pile et al. 2019). A recent study quantifying mortality during this period found that ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), the dominant canopy tree species in many low- and mid-elevation forests in the Sierra Nevada, experienced the highest rate of mortality relative to co-existing species like incense cedar (*Calocedrus decurrens*) (Fettig et al. 2019). At sites ranging from ~900- to 2200-m elevation in four national forests in the Sierra Nevada, ponderosa pine had an 89.6% mortality rate compared to only 23.2% for incense cedar. The highest mortality rates occurred at lower elevations

(~1100 m), with many sites experiencing 100% ponderosa pine mortality (Fettig et al. 2019). Large-scale mortality of a dominant canopy tree species like ponderosa pine could have substantial and widespread effects on forest structure, species composition, biodiversity, and ecosystem function in California and across the western United States (van Mantgem 2009; Adams et al. 2010; Anderegg et al. 2015).

Increasing hydroclimate variability and drought severity across much of the western United States is projected to continue (Yoon et al. 2015; Cook et al. 2020) and will likely result in more large-scale forest mortality events that threaten the long-term viability of ponderosa pine and other ecologically and economically important tree species across warmer and drier parts of their species distributional ranges (Allen et al. 2010; Williams et al. 2020). As the climate warms, ponderosa pines are also affected by increasing frequency and severity of disturbance, including outbreaks of western pine beetle (*Dendroctonus brevicomis*; WPB) (Kolb et al. 2016a) like the one that occurred during the CA Drought (Fettig et al. 2019). In California, WPBs are capable of producing two, or sometimes three, generations per year depending on the length and temperature of the growing season (DeMars and Roettgering 1982). In other bark beetle species, higher minimum winter temperatures can also result in less over-winter death (Bentz et al. 2010), and warm spring and summer temperatures can result in earlier WPB adult emergence, increasing the potential for a successful third generation (Miller and Keen 1960). In these ways, climate warming can directly and positively influence WPB population sizes.

Climate warming may also indirectly affect WPB success by influencing ponderosa pine vigor and defensive capacity. While mild or moderate drought stress may increase the allocation of carbon resources to defense, severe drought stress often results in stomatal closure and reduced photosynthesis, and/or failures in the phloem system, all of which can lead to carbon starvation and insufficient resources for defense (Kolb et al. 2016a; McDowell et al. 2011; Sevanto et al. 2014). Severe drought stress in trees is thought to increase susceptibility to bark beetle attacks (Raffa et al. 2008; Gaylord et al. 2013; Kolb et al. 2016b). Kolb et al. (2019) recently found experimental evidence of drought stress increasing ponderosa pine susceptibility to WPB-induced mortality, whereby mortality was highest in trees that experienced concurrent water stress and bark beetle attack. Stephenson et al. (2019) also found that larger ponderosa pines generally experience higher mortality rates during bark beetle outbreaks, indicating that beetle-induced mortality in ponderosa pines is strongly driven by host selection. Additionally, aspects of stand structure and competition that can affect a tree's vigor and ability to mobilize carbon defenses are known to impact survival during large beetle outbreaks (Waring

and Pitmann 1985; Coops et al. 2009; Fettig et al. 2019). A better understanding of these relationships could inform future management practices—such as prescribed burning and variable density thinning (Churchill et al. 2013; Hessburg et al. 2016)—aimed at improving forest resistance and resilience in the face of future disturbance.

Responses to drought using tree ring widths and stable isotope analyses of tree-ring cellulose have been used extensively to gain insight into past climate conditions and ponderosa pine response to climate variability (McDowell et al. 2003; Roden and Ehleringer, 2007; Williams et al. 2010, 2012; Leavitt et al. 2011; Szejner et al. 2016; Voelker et al. 2019; Ulrich et al. 2019). Tree-ring carbon isotope discrimination ($\Delta^{13}\text{C}$) is largely determined by the ratio of photosynthetic assimilation to stomatal conductance (Farquhar et al. 1989; Ehleringer et al. 1993). Therefore, $\Delta^{13}\text{C}$ of the latewood component of tree-rings can be used to infer severity of inter-annual drought stress when leaf gas exchange is primarily limited by stomatal conductance during dry summer conditions—conditions that are prevalent across much of the western US (McDowell et al. 2003; Voelker et al. 2019). In ponderosa pine, tree-ring $\delta^{18}\text{O}$ signals can be strongly affected by differences in source water $\delta^{18}\text{O}$ due to how rooting depth is modified by tree age or competition among dead and surviving trees (Kerhoulas et al. 2013), and also by regional climate across the western United States (Roden and Ehleringer 2007; Szejner et al. 2016; Belmecheri et al. 2018). Recent efforts have also linked increasing aridity to increasing tree-ring $\delta^{18}\text{O}$ and inferred reduced stomatal conductance at these sites (Guerreri et al. 2019). Therefore, tree-ring $\delta^{18}\text{O}$ can potentially yield insights on whether there are relevant physiological differences in drought stress or rooting depth among groups of trees that is independent from tree-ring $\Delta^{13}\text{C}$ and growth.

To seek a stronger understanding of what ecophysiological responses to drought stress, if any, determined susceptibility to beetle attack during the recent California drought and associated WPB outbreak, we employed annually resolved ring widths and stable isotope data from six pairs of ponderosa pines that died vs. survived. The specific objectives of this study were to determine whether surviving vs. dead trees differed in (1) growth rates, (2) absolute level of $\Delta^{13}\text{C}$ or $\delta^{18}\text{O}$, or (3) sensitivity of $\Delta^{13}\text{C}$ or $\delta^{18}\text{O}$ to drought-related climate variables, and (4) whether stand density affected growth rates or stable isotope sensitivity to climate. Overall, this study sought to determine whether any differences in ecophysiology over time could help explain the ability of a certain few overstory ponderosa pines to survive severe drought conditions and a concurrent WPB outbreak while a much larger proportion of ponderosa pines died in association with the CA Drought (Fettig et al. 2019; Pile et al. 2019).

Materials and methods

Study area

Sampling for this project was conducted in the spring of 2017 at Soaproot Saddle, a Southern Sierra Critical Zone Observatory (SSCZO) site northeast of Fresno, CA (Fig. 1). In this area, ponderosa pine-dominated mixed conifer forests occur between ~900- and 2,000-m elevation. Other common species in this region include incense cedar (*C. decurrens*), California black oak (*Quercus kelloggii*), sugar pine (*Pinus lambertiana*), Douglas fir (*Pseudotsuga menziesii*), and manzanita (*Arctostaphylos* spp.). Soaproot Saddle is located at 1160 m elevation and receives ~800 mm of precipitation each year. Mean minimum temperature in this region is 5.5 °C and mean maximum temperature is 18 °C (Goulden et al. 2012). A large portion of annual precipitation occurs in the winter and spring, followed by a summer drought period. Historically, this ecosystem experienced frequent, low-intensity fires every 10–20 years that kept ponderosa pine-dominated forests “open and parklike” (Parsons and DeBenedetti 1979; North et al. 2005; Van de Water and Safford 2011; Hood et al. 2016). Since widespread fire suppression efforts have been in place over the past century, many forests in this region have transitioned to dense, mixed-conifer forests with higher populations of fire-intolerant and shade-tolerant understory species (Stephens et al. 2015). However, fire-scars on tree stumps cut in 2016 from a stand centrally located among the trees sampled for this study showed at

least two surface fires had burned in this area approximately 38 and 53 years prior to our 2017 sampling, indicating that surface fires during the second half of the twentieth century likely contributed to the patchy distribution of basal area characterizing this area (S. Voelker, Pers Obs).

Field Data Collection

Pairs of surviving and dead ponderosa pines were selected based on their similar stature, estimated age, and proximity to one another; average distance between paired trees was ~75 m. Individuals selected as focus trees were visually estimated to be > 100 years old and then this was confirmed upon ring counts when cores were extracted. Pairs of trees were also chosen for similarity of growing conditions (i.e. slope, geomorphic position, and density of understory vegetation). Six pairs of surviving and dead trees were sampled (12 total focus trees) and three 12 mm-diameter increment cores were extracted from each focus tree at breast height (between 1.0 and 1.5 m from ground level). Focus tree DBH, height, age, and basal area measurements for each plot can be found in Table S1.

A 15 m-radius fixed-area circular plot was established with each focus tree at the center. Information recorded for trees ≥ 20 cm DBH (diameter at breast height) within each plot included DBH, species, and status (surviving/dead and evidence of WPB attack when applicable). Basal area was calculated for each fixed-area plot (15-m radius) using the following equation:

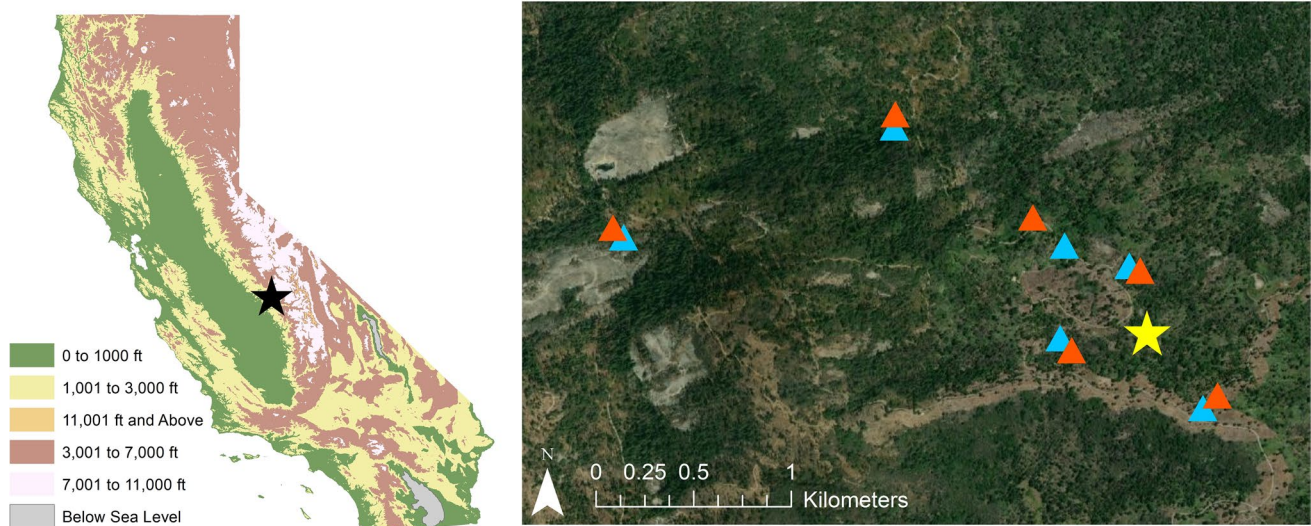


Fig. 1 Left Panel: Location of the Soaproot Saddle field site (black star) in central California (37.03 N, 119.25 W) (Source: Conservation Biology Institute). Right Panel: Plot locations at Soaproot Saddle. Blue triangles represent plots with surviving focus trees, red triangles represent plots with dead focus trees. Surviving and dead focus tree

plots in close proximity are paired trees. White crosses represent trees randomly sampled in 2015 by Ferrell (2017) (Sources: Esri, Digital-Globe, Earthstar Geographics, CNES/Airbus DS, GeoEye, USDA FSA, USGS, AeroGrid, IGN, IGP, and the GIS User Community). This figure is available in color in the online version of the journal

$$BA = \frac{\sum DBH^2 * 0.00007854}{Area} \quad (1)$$

Total basal area, including all species present in the plot, was calculated as well as basal area of ponderosa pine at each plot.

Additional increment cores from ponderosa pines sampled by Ferrell (2017) were also utilized in order to compare the focus trees in this study to a random sample of ponderosa pines that also grew at Soaproot Saddle. Of all cores sampled by Ferrell (2017) we only used cores from trees > 100 year of age. Locations of these randomly sampled trees relative to our focus trees are shown in Fig. 1 (mean size and age of these trees are listed in table S2).

Increment core preparation and measurements

Each increment core was mounted on a wooden stave and sanded using increasingly higher-grit sand paper (120–400) to prepare cores for visual cross-dating and measurement of annual growth rings. Whole ring widths as well as separate early- and latewood widths were measured using MeasureJ2X software (Voortech Consulting). Visual cross-dating was then conducted to assign calendar years to the rings in each core (Stokes and Smiley 1968). Visual cross-dating between trees was confirmed using COFECHA, a statistical program that assesses cross-dating quality and accuracy (Holmes 1983). Ring width chronologies for each focus tree were detrended separately using a negative exponential spline first to remove the biological growth signal, then with a cubic smoothing spline set to a 50% frequency–response cutoff of 100 years to isolate inter-annual to decadal climate variation from age-related changes in growth (Bunn 2008). All detrending was conducted in ARSTAN (Cook and Krusik 2014).

DBH and ring widths were used to calculate basal area increment (BAI) for focus trees and randomly sampled trees to determine annual growth rates. BAI was employed because it has been shown to be strongly related to biomass increment across forest types, climates, and management regimes (Babst et al. 2014). BAI was calculated from the outside-in, assuming circularity of the growing cambium and employed estimates of bark thickness (McDonald 1983; Larsen and Hann 1985) to adjust for differences in radial measurements inside and outside of the bark for each tree. To minimize the potential for bias in assessing growth rates for trees that differed among groups in DBH, the age-related trend in BAI for randomly sampled trees was calculated using Eq. (2) ($R^2 = 0.90$, $p < 0.01$; data not shown). Thereafter, BAI deviations (BAI_D) were calculated for each tree using Eq. (3).

$$\text{PredictedBAI} = 0.8751 * \text{Age}^{0.6304} \quad (2)$$

$$BAI_D = \frac{\text{Observed BAI} - \text{Predicted BAI}}{\text{Predicted BAI}} * 100 \quad (3)$$

This approach to removing age-related trends from growth data, often termed regional chronology standardization (RCS), has often been employed in the field of dendroclimatology (Briffa and Melvin 2011), and more relevant to this study, has also been used to determine differences in growth rate among sites or sampling conditions within the same tree species while accounting for tree age (Voelker 2011; Voelker et al. 2014). As noted from Eq. (2), BAI increased strongly with age in the ponderosa pines we sampled randomly, prior to mortality from the WPB outbreak. These trees were used to determine a baseline for the trend in age-related BAI in Eq. (2) because we explicitly wanted to test whether surviving or dead trees, selected after beetle-induced mortality, may differ in growth rates compared to a random sampling scheme. In Eq. (3) we divided the BAI residuals (i.e., *Observed BAI*—*Predicted BAI*) by *Predicted BAI* to avoid the problem of unstable variance that is produced when removing the effect of growth rate due to cambial age via this type of regional chronology standardization (Helama et al. 2004).

Stable isotope analysis

For each core from the 12 focus trees (three cores per tree), latewood for the years 1950–2016 was separated using a scalpel under a dissecting microscope. For each individual tree, latewood from the three cores was combined for each year, creating one set of latewood samples per focus tree that spanned the years 1950–2016. Samples were then ground to a fine powder and sealed in a mesh filter bag (mesh size 25 µm; ANKOM Technology, Macedon, NY). Samples were bleached using sodium chlorite and glacial acetic acid to remove extractives from the wood, leaving only holocellulose (Leavitt and Danzer 1993). Next, sodium hydroxide and glacial acetic acid were used to remove hemicellulose and yield α-cellulose, which faithfully records the $\delta^{18}\text{O}$ signature recorded in the wood each year without exchanging with atmospheric water (Rinne et al. 2005). After isolating α-cellulose, each sample was homogenized in deionized water using an ultrasonic probe and subsequently freeze-dried (Laumer et al. 2009). Samples were then packed in tin ($\Delta^{13}\text{C}$) or silver ($\delta^{18}\text{O}$) capsules before being analyzed at the Center for Isotope Biogeochemistry (CSIB) at the University of California, Berkeley. The carbon isotope ratio of each sample was obtained using standard high-temperature combustion in a vario-Pyrocube elemental analyzer interfaced with an IsoPrime/Elementar IsoPrime

100 gas phase isotope ratio mass spectrometer (IsoPrime Ltd., Manchester, UK). The oxygen isotope ratios were determined by pyrolyzing α -cellulose in an elemental analyzer (TC/EA, IsoPrime/Elementar vario-Pyrocube) and analyzing the resulting gas with an isotope ratio mass spectrometer (IsoPrime 100). The long-term precision does not exceed ± 0.1 ‰ for $\delta^{13}\text{C}$ and 0.2 ‰ for $\delta^{18}\text{O}$ for the mass spectrometer employed at CSIB.

All $\delta^{13}\text{C}$ values were converted to carbon isotope discrimination values ($\Delta^{13}\text{C}$) following Farquhar et al. (1982):

$$\Delta^{13}\text{C} = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}}{1 + \delta^{13}\text{C}_{\text{plant}}/1000} \quad (4)$$

In this equation, $\delta^{13}\text{C}_{\text{air}}$ was estimated annually from the values given by McCarroll and Loader (2004) and merged seamlessly with more recent $\delta^{13}\text{C}_{\text{air}}$ records from Mauna Loa, Hawaii. $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope series that were intended for comparison to climate variability were detrended with ARSTAN software (Cook and Kruskal 2014) using a cubic smoothing spline set to a 50% frequency–response cutoff of 100 years to isolate inter-annual to decadal climate trends from low-frequency variation that could arise due to changes in competition, tree height, or rooting depth. “Residual” isotope series were then multiplied by the mean isotopic value for each core to obtain a pre-whitened isotope series in permil (‰) units and without autocorrelation for each focus tree. Due to poor statistical cross-dating of two isotope time series (Roden 2008), these data were removed from subsequent statistical analyses, resulting in a sample size of ten trees.

Climate data

The climate data employed were obtained through PRISM (<https://prism.oregonstate.edu/>) and ClimateWNA (<https://www.climatewna.com/>). Palmer Drought Severity Index (PDSI) data for California’s 5th climate division was obtained through the National Oceanic and Atmospheric Association (NOAA). Climate variables, including PDSI, vapor pressure deficit (VPD), climatic moisture deficit (CMD), and precipitation were seasonally averaged for winter (previous December, current January and February), spring (March, April, May), summer (June, July, August), and fall (September, October, November). Seasonal climate data from 1950 to 2016 were pre-whitened using the same procedure employed for tree-ring data, which removed autocorrelation and long-term trends and highlighted inter-annual variation.

Statistical analyses

Pre-whitened climate series were compared to similarly pre-whitened isotope chronologies for the years 1950–2016 and Pearson’s correlation coefficients were calculated. Correlations were calculated separately for surviving and dead focus trees. 20-year moving window correlations were conducted for each climate variable with the $\Delta^{13}\text{C}$ record using the tidyquant package in R (Dancho and Vaughan 2018). To determine whether significant isotopic differences ($\Delta^{13}\text{C}$ or $\delta^{18}\text{O}$) exist between surviving and dead trees, we employed repeated measures mixed effects modeling using the package nlme in R (Pinheiro et al. 2015). Focus tree pair (1–6) was included as a random variable with year, status (surviving or dead), and their interaction as predictors. To test for differences in growth rates, a repeated measures mixed effects model was conducted for BAI_D with the same random and predictor variables. Trees sampled by Ferrell (2017) and exceeding 100 years of age were included in this model. Similarly, a linear mixed effects model was used to compare basal area and percent dead ponderosa pine between plots with surviving and dead focus trees. Focus tree pair was included as a random variable and focus tree status (surviving or dead) as the predictor variable. Additionally, F -tests were used on pre-whitened isotope series to determine whether inter-annual variance in $\Delta^{13}\text{C}$ or $\delta^{18}\text{O}$ differed among surviving and dead focus trees.

Results

All dead focus trees had evidence of WPB attack, including pitch tubes, entrance holes, and gallery excavations, but we found no evidence of WPB attack on any of the surviving focus trees. This indicates that WPB attacks and subsequent effects of mycangial blue stain fungal associates (*Entomocorticium* sp. B and *Ceratocystiopsis brevicornis*; Bracewell and Six 2014) on xylem and phloem functionality were the ultimate causes of mortality, even though essentially all trees underwent moderate to severe drought stress. DBH was greater in surviving trees than in dead trees ($p=0.03$), but tree age was not different between the two groups ($p=0.20$).

Across the entire 1900–2016 period, ponderosa pines that survived the CA Drought and WPB outbreak had significantly higher BAI_D than trees that died ($p<0.01$) (Fig. 2). Although both groups of trees show a steep decline in growth rate during the drought, surviving trees displayed a slight uptick in growth during 2016 after this region received substantial precipitation during the previous winter. Other notable periods of low growth rates include severe multi-year droughts during 1987–1992 and 1929–1934, the latter being associated with the dust bowl droughts that affected much of North America (Jones

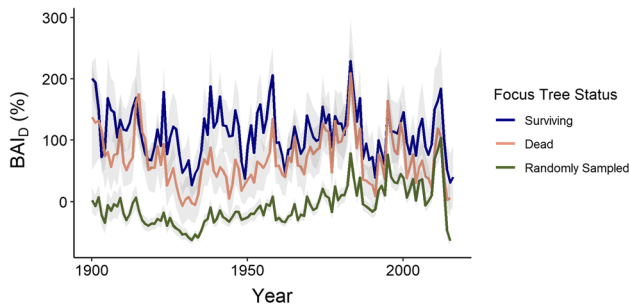


Fig. 2 BAI deviations (BAI_D) (%) for surviving (blue), dead (red), and randomly sampled (green) ponderosa pines from 1900 to 2016. This figure is available in color in the online version of the journal

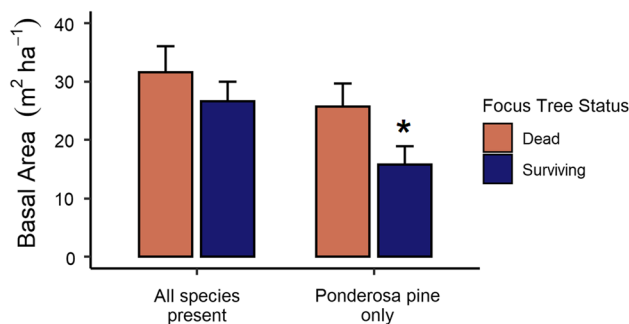


Fig. 3 Basal area of all species present and ponderosa pine only in plots with a dead vs. surviving focus tree. Stars indicate significant differences between groups. Error bars represent standard error. This figure is available in color in the online version of the journal

2015). Compared to tree core data collected at random locations across the same watershed by Ferrell (2017), both live and dead focus trees sampled in this study grew consistently faster since 1900. These randomly sampled trees also experienced a steep decline in growth during the CA Drought (Fig. 2). The randomly sampled trees had a mean DBH of 47.2 cm (± 16 SD) and mean age of 115.3 years (± 38 SD) (Table S1). In contrast, pairs of ponderosa pines selected for this study were substantially larger (85.2 cm ± 20.4 SD) and older (162.1 years ± 40.7 SD) on average.

Plot-scale basal area, including all species present within each plot, was compared between plots with a surviving focus tree and plots with a WPB-killed focus tree. There was no significant difference in total plot basal area between the two groups of plots when all tree species were included ($p=0.55$). However, there was significantly greater ponderosa pine basal area at plots associated with a dead focus tree ($p=0.01$) and higher percent ponderosa pine mortality in plots with a dead focus tree ($p<0.01$) (Fig. 3). Additionally, plots with a dead focus tree had 100% mortality of ponderosa pines > 30 cm DBH.

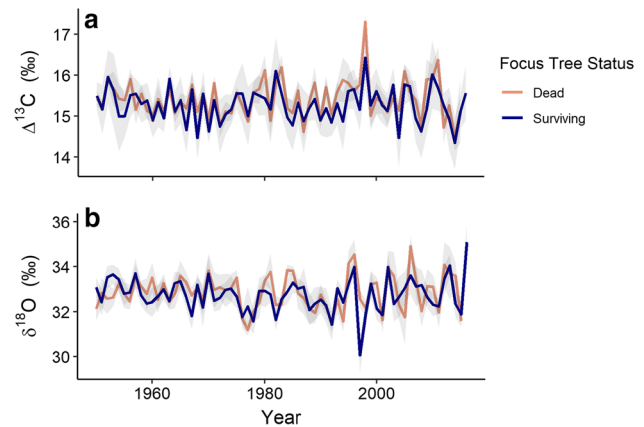


Fig. 4 Pre-whitened latewood (a) $\Delta^{13}C$ and (b) $\delta^{18}O$ data for the years 1950–2016 separated by focus tree status (surviving or dead). Error ribbons for each record represent standard error. This figure is available in color in the online version of the journal

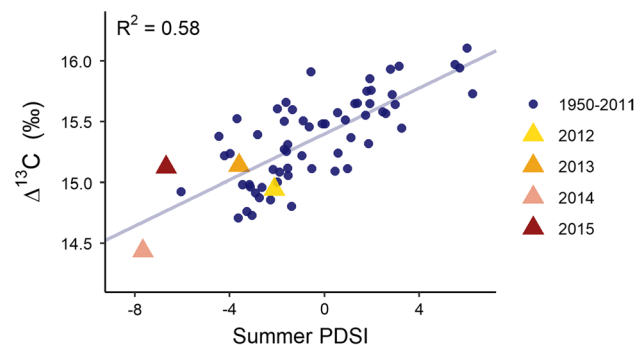


Fig. 5 Latewood $\Delta^{13}C$ values compared to summer PDSI for the years 1950–2015. Drought years (2012–2015) are represented by triangles and all other years (1950–2011) are represented by blue circles. This figure is available in color in the online version of the journal

Interestingly, there were no significant differences in latewood $\Delta^{13}C$ or latewood $\delta^{18}O$ between trees that survived and trees that were killed by WPB during the drought ($p=0.99$ and $p=0.16$, respectively) from 1950 to 2016 (Fig. 4a–b). Dead focus tree $\Delta^{13}C$ showed elevated inter-annual variance compared to surviving focus trees (dead = 0.22 ‰; surviving = 0.17 ‰) but the difference was not significant ($p=0.33$). Variance in dead focus tree $\delta^{18}O$ (1.52 ‰) was significantly higher than in surviving focus trees (0.65 ‰) ($p<0.01$). When compared to spring and summer PDSI from 1950 to 2016, $\Delta^{13}C$ values were near their lower extreme during the CA Drought, particularly during 2014 which had the lowest PDSI and $\Delta^{13}C$ values for this time period (Fig. 5).

Of the four drought-related climate variables we report upon here (PDSI, VPD, CMD, and precipitation), only PDSI had significant correlations with $\delta^{18}O$, and only with dead

focus trees during the spring and summer (Table 1a). Overall, $\delta^{18}\text{O}$ was poorly correlated with drought-related climate variables during this time period. $\Delta^{13}\text{C}$ was positively correlated with PDSI and precipitation and negatively correlated with VPD and CMD (Table 1b). The highest correlations between $\Delta^{13}\text{C}$ and VPD, CMD, and precipitation were associated with the spring season, but $\Delta^{13}\text{C}$ was more closely related to PDSI during the summer season. This pattern of response was consistent in both surviving and dead ponderosa pines. $\Delta^{13}\text{C}$ correlation strengths were similar for both groups of trees, although live focus trees had slightly stronger spring correlations for most climate variables.

Discussion

As temperatures have continued to warm across the western United States over the past several decades, aridity and drought events have become more frequent and severe (Allen et al. 2010). Warmer, drier conditions have resulted in longer growing seasons and earlier snowmelt in California (Gleick 1987; Stewart et al. 2004; Mote et al. 2005), and drought sensitivity of ponderosa pines in the Sierra Nevada has increased over the past century (Keen 2019). PDSI and $\Delta^{13}\text{C}$ values were both near low extremes during the CA Drought compared to the rest of the 1950–2016 period, particularly during 2014 (Fig. 5), indicating that stomatal constraints on canopy-integrated leaf gas exchange in these ponderosa pines closely tracked the severity of the California drought.

The strongest differences between surviving and WPB-killed ponderosa pines found in this study was in growth rate. Relatively old and large trees that managed to survive

the CA Drought and concurrent WPB outbreak in this area grew significantly faster than those that were killed (Fig. 2), even though pairs were located in close proximity. The influence of growth rate on susceptibility to attack by a variety of bark beetle species can depend upon elevation, climate conditions, and stand age (Cooper et al. 2018). The few studies that have specifically investigated how growth rates of ponderosa pine may influence attacks and/or mortality by WPB have found that large, slower-growing trees are preferentially attacked under endemic beetle conditions and at the beginning of an epidemic-scale outbreak (Craighead 1925; Person 1928; Miller and Keen 1960) like that which afflicted the Sierra Nevadas during the CA Drought. Mountain pine beetle (*Dendroctonus ponderosae*; MPB), another bark beetle species that attacks ponderosa pine in the western United States, has been studied more extensively, and yet the relationship between tree growth rate and mountain pine beetle attack success is still not clear. Multiple studies have shown that MPB preferentially attacks faster growing trees (Yanchuk et al. 2008; Margoles 2011; de la Mata et al. 2017) while others have shown the opposite trend (Waring and Pitman 1985; Coops et al. 2009; Knapp et al. 2013; Cooper et al. 2018).

In this study, pairs of large, old ponderosa pines were selected for sampling, so these trees do not necessarily represent the larger population of ponderosa pines in this area. Growth rates from our focus trees were compared to a more extensive sampling of tree cores from this watershed, which was undertaken in 2015 (Ferrell 2017) before most trees had died. BAI data were calculated for a sub-set of these trees exceeding 100 years of age so that the results would be comparable to the trees sampled in this study. These randomly

Table 1 Pearson's correlation coefficients for (A) $\Delta^{13}\text{C}$ and (B) $\delta^{18}\text{O}$ records compared to multiple climate variables

(A) $\Delta^{13}\text{C}$	Surviving focus trees				Dead focus trees			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
PDSI	0.49*	0.68*	0.73*	0.58*	0.56*	0.68*	0.73*	0.61*
VPD	– 0.19	– 0.68*	– 0.41*	– 0.15	– 0.33*	– 0.52*	– 0.46*	– 0.18
CMD	– 0.03	– 0.65*	– 0.35*	– 0.21*	– 0.15	– 0.49*	– 0.44*	– 0.10
Precip	0.26*	0.59*	0.21*	0.04	0.40*	0.52*	0.28*	– 0.04
(B) $\delta^{18}\text{O}$	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
PDSI	0.02	0.01	0.03	– 0.12	0.21*	0.27*	0.32*	0.19
VPD	– 0.07	0.04	– 0.09	0.06	– 0.13	– 0.17	0.04	0.09
CMD	– 0.22*	0.04	– 0.05	0.15	– 0.14	– 0.14	0.05	0.22*
Precip	– 0.07	– 0.07	– 0.02	– 0.08	– 0.02	– 0.16	– 0.05	– 0.21*

Data used for correlations include pre-whitened isotope data and residual climate data (detrended to remove long-term directional trends). Monthly climate data were averaged by season (Winter—DJF, Spring—MAM, Summer—JJA, Fall—SON) and compared to long-term isotope data for the same years (1950–2016). Significant correlations with p -values < 0.05 (≥ 0.24 or ≤ -0.24) and are denoted by (**). Correlations with p -values < 0.1 (≥ 0.20 or ≤ -0.20) are denoted by (*). P -values for all correlations are shown in Table A-2

sampled trees had substantially lower growth rates compared to both surviving and dead focus trees sampled for this study. Hence, our dead focus trees exhibited growth rates that were faster than average for trees of a comparable age distribution, and our surviving trees grew faster yet than both of the previous groups. Since dead focus trees were growing in close proximity to surviving focus trees, it is clear that soil and stand conditions that promoted higher productivity also tended to favor the survival of faster growing trees on such plots. Overall, the CA Drought and concurrent WPB outbreak was so severe across our study area that only the fastest of the fast-growing large, overstory ponderosa pines survived. Note that many more small ponderosa pines (i.e. < 30 cm DBH) survived compared to large ones, but only in plots with a surviving focus tree (Fig. 3) and presumably favorable growing conditions. However, this is likely not a consequence of tree size per se, but of the success of beetle brood production in trees with greater phloem thickness (Amman 1972; Graf et al. 2012), a trait which is strongly correlated with tree size as small trees tend to grow slower due to their subordinate status in closed canopy stands. Indeed, our findings from intensive growth and stable isotope measurements on a small number of trees are supported by more extensive forest inventory efforts that overlap with our Soaproot Saddle sampling location. In particular, Pile et al. (2019) also found that larger size in ponderosa pines was consistently associated with increased survival following the CA Drought and WPB outbreak.

During a less severe drought and/or bark beetle outbreak, it is possible that the threshold growth rate for overstory tree survival would have been lessened where drought stress and associated beetle pressure were lower (Craighead 1925; Person 1928; Miller and Keen 1960). Although the randomly sampled trees (Ferrell 2017) were alive during sampling in summer of 2015, and we do not have data on their post-drought status, ~50% of these trees had missing rings in 2014 and 2015, suggesting that growth had slowed or ceased for half of all sampled trees during the drought. Given that Fettig et al. (2019) found that ~89% of ponderosa pines > 30 cm DBH died during the drought, it is likely that the majority of the trees that were alive and sampled randomly during the summer of 2015 (Ferrell 2017) died shortly thereafter. Further insights on this particular sequence of mortality was provided by Pile et al. (2019), who showed that the probability of a ponderosa pine surviving the drought through 2015 varied between ~60 and 90% depending on DBH, whereas the same trees sampled in 2017 varied in survival between ~10 and 30%.

Although we expected to see faster growth rates in surviving large ponderosa pines, we anticipated that it would be accompanied by lower severity of drought stress relative to trees that were killed by WPB during the drought. However, we found no evidence of differences in absolute $\Delta^{13}\text{C}$ and

$\delta^{18}\text{O}$ values or in the sensitivity to drought-related climate variables that may have suggested that stomatal constraints on leaf gas exchange differed between surviving and dead focus trees. According to theory underlying stable carbon isotopes (Farquhar et al. 1989; Dawson et al. 2002; McCarroll and Loader 2004), and stable oxygen isotopes (Edward and Fritz 1986; Farquhar and Lloyd 1993; Roden et al. 2000; Barbour et al. 2004), higher sensitivity to drought stress would have presented as lower $\Delta^{13}\text{C}$ values, higher $\delta^{18}\text{O}$ values, and stronger climate correlations in the dead focus trees relative to surviving focus trees. Instead, our results show that both groups of trees have had very similar $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ records for the past ~65 years (Fig. 4) and appear to be responding to climate in a similar way based on similar correlation strengths with drought-related climate variables (Table 1). Moreover, Keen (2019) investigated $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ across three sub-annual divisions within each ring spanning 1997 to 2016 and found no detectable differences in isotopic variability or sensitivity to climate between surviving and dead trees in the decades leading up to the CA Drought (R. Keen, *unpublished analyses*).

The relatively weak correlations between $\delta^{18}\text{O}$ and these variables is likely due to winter precipitation typically serving as the primary water source for many tree species, and increasingly so in dry habitats (Allen et al. 2019). This water-use strategy could result in a tree-ring $\delta^{18}\text{O}$ record that primarily reflects the values of source water winter precipitation $\delta^{18}\text{O}$ instead of evaporative enrichment during the growing season. As recent and past hydroclimatic variability across the US West Coast has shown, the location of dominant storm tracks can greatly modify the geography and intensity of winter precipitation from year to year (Wise and Dannenberg 2017; Eldardiry et al. 2019). These shifts in atmospheric circulation can induce changes in precipitation $\delta^{18}\text{O}$ of individual storms on the order of 5 ‰ (Smith et al. 1979). These major storms could increase the influence of source water $\delta^{18}\text{O}$ variability and dampen the expected influence of drought stress and stomatal closure on tree-ring $\delta^{18}\text{O}$ compared to what would be expected if source water $\delta^{18}\text{O}$ were constant.

Among the pairs of surviving and dead trees, meteorological conditions would have been more or less constant, but it is possible that belowground conditions not easily recognized as hydrologic refugia (sensu McLaughlin et al. 2017) could have still differentiated these groups since we found that dead trees had greater tree-ring $\delta^{18}\text{O}$ variability. It is difficult to ascertain the importance of this potential influence with the retrospective data available. However, had this belowground microsite-effect been important for determining tree ecophysiology to the extent that it shifted susceptibility to bark beetles, it should also have been reflected in differences among groups in the absolute value of tree-ring $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ and/or the strength of correlations with

drought related climate variables. Therefore, differences between surviving and dead trees seem likely to have been linked to genes that influenced growth rates and defensive traits without having modified leaf gas exchange. This is a somewhat puzzling, but potentially important, conclusion, as factoring out differences in leaf gas exchange severely constrains the list of potential genetic influences on growth processes that may also be linked to defense. Overall, due to the severity of the CA Drought and the very low $\Delta^{13}\text{C}$ values we demonstrated, it is likely that ponderosa pines underwent widespread and significant drought stress. Whether that drought stress was strong enough to make most trees more susceptible to WPB attack (Raffa and Berryman 1983; Anderegg et al. 2015; Kolb et al. 2019) is not firmly established, but a scenario of widespread increases of host susceptibility in response to drought stress would be consistent with the extreme nature of the meteorological drought severity (Griffin and Anchukaitis 2014) as well as the most severe WPB outbreak in recorded history (Fettig et al. 2019).

A possible explanation for the observed discrepancy in growth rates between surviving and dead focus trees is differences in growth-defense strategies. Carbon fixation is hypothesized to be greater in faster growing trees, thereby providing a surplus of carbon for secondary metabolites including physical and chemical defenses (Waring and Pitmann 1985; McDowell et al. 2007). Another hypothesis suggests that resource limitations (e.g., water and nutrients) that reduce growth more than photosynthesis will increase carbon allocation to defenses with little or no tradeoffs in growth, while higher allocation of resources to relative growth rate when resource availability is high will result in a tradeoff and lower allocation of resources to defenses (Herms and Mattson 1992; Stamp 2003). There are examples providing support for both hypotheses in pines (Kane and Kolb 2010; Ferrenberg et al. 2014; Hood and Sala 2015; Hood et al. 2015; Gaylord et al. 2015; Moreira et al. 2014), highlighting how genetic variation among individuals and a complex suite of climatic and environmental conditions can influence carbon allocation to growth and defense (Rigling et al. 2003; Kichas et al. 2020). Although we did not directly measure defense traits, we observed no signs of WPB attack on our surviving focus trees, which were also the individuals that were growing the fastest. Without any signs of attack on surviving trees, increased resin defenses associated with high growth rates (Kane and Kolb 2010; Hood and Sala 2015) do not seem to have been an important deterrent. Rather, these results support Kichas et al. (2020) who suggested a potential role of growth-related defense traits in host identification and selection by bark beetles.

In combination with Kichas et al. (2020), our findings that fast growth rates in trees conferred resistance to a drought- and beetle attack-induced demographic bottleneck may be important for understanding the evolution of pines and other

conifer hosts of bark beetles. The increasingly common refrain of large trees being more susceptible to drought and/or bark beetles (Bennett et al. 2015; Stephenson et al. 2019; Stovall et al. 2019) could, at first glance, suggest that suites of growth and defensive traits associated with smaller stature or slower growth may be overwhelmingly passed on to trees regenerating after such large bottleneck events. However, because large, dominant, and fast-growing ponderosa pines tend to produce vastly more cones and on a more consistent basis than small and mid-canopy or suppressed ponderosa pines (Krannitz and Duralia 2004), their survival will also influence the next generation. Ponderosa pine regeneration in areas within the footprint of the CA Drought will certainly derive from some admixture of currently small and slow-growing vs. large and fast-growing trees. Understanding the balance of what suites of growth and defensive traits are preferentially passed on following these bottleneck events needs further investigation.

In addition to having faster growth rates, surviving trees in this study also grew in plots that contained significantly less ponderosa pine basal area compared to plots with a dead focus tree ($p=0.01$). Again, wider forest inventory efforts following the CA Drought support our finding that the probability of survival for ponderosa pines was tied to the amount of ponderosa pine basal area at a given plot (Pile et al. 2019). However, we also found that total plot basal area did not significantly impact survival (Fig. 3). Similarly, Pile et al. (2019) showed that ponderosa pine survival was actually bolstered by higher overall forest basal area. These results collectively suggest that total competition was not a strong factor in mortality of ponderosa pines during the outbreak phase of beetle attacks, but that host availability and/or the degree of local clustering of ponderosa pines did impact survival during and following the CA Drought and WPB outbreak.

Conclusion

In this study, located near the epicenter of drought severity during the CA Drought, we compared inter-annual variation in growth rates and tree-ring $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ between ponderosa pines that survived and those that were killed by WPB. Comparisons among surviving and dead trees for ~65 years preceding the drought revealed no evidence for differences in the degree of stomatal constraints on leaf gas exchange (i.e., absolute $\Delta^{13}\text{C}$, one dimension of drought stress), or differences in depth of root water uptake. Because $\Delta^{13}\text{C}$ did not differ, $\delta^{18}\text{O}$ could only have been influenced by depth of root water uptake, and there were no differences in $\delta^{18}\text{O}$. We also found no differences between surviving and dead trees in sensitivity of tree-ring $\Delta^{13}\text{C}$ and $\delta^{18}\text{O}$ to drought-related climate variables. Collectively, these results

indicate that factors outside of soil water availability had a stronger influence on tree survival during a historic drought and beetle outbreak. Surviving trees had higher growth rates and grew in plots with lower ponderosa pine basal area than trees that were killed by WPB, and these findings are supported by wider forest monitoring efforts in the southern Sierra Nevadas (Pile et al. 2019). Altogether, the small number of large ponderosa pines that did survive such a severe drought and WPB outbreak were the fastest growing trees on productive sites that were relatively isolated from conspecific host species, which likely provided a buffer from WPB population sources.

Acknowledgements We wish to thank the Southern Sierra Critical Zone Observatory (SSCZO) for maintenance of the Soaproot Saddle field site. We specifically thank Erin Stacy from the CZO and Beverly Bulaon from the Forest Service for their assistance with site selection and sampling, and Mike Goulden for substantial information regarding the ecology and history of Soaproot Saddle.

Author contribution statement RMK and SLV designed the experiment and collected data with help from BJB. RMK performed laboratory analyses. RMK and SLV performed data analysis, with substantial input and assistance from SYW and BJB. RF provided additional tree cores from Soaproot Saddle and assisted with data interpretation. All authors significantly contributed to data evaluation and manuscript preparation and gave final approval for publication.

References

- Adams HD, Macalady AK, Breshears DD, Allen CD, Stephenson NL, Saleska SR, Huxman TE, McDowell NG (2010) Climate-induced tree-mortality: earth system consequences. *Eos Trans Am Geophys Union* 91:153–154
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Venetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manage* 259:660–684
- Amman GD (1972) Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *J Econ Entomol* 65:138–140
- Anderegg WL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz BJ, Hood S, Lichstein JW, Macalady AK, McDowell N, Pan Y, Raffa K, Sala A, Shaw JD, Stephenson NL, Tague C, Zeppel M (2015) Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol* 208:674–683
- Babst F, Bouriaud O, Alexander R, Trouet V, Frank D (2014) Toward consistent measurements of carbon accumulation: A multi-site assessment of biomass and basal area increment across Europe. *Dendrochronologia* 32(2):153–161
- Barbour MM, Roden JS, Farquhar GD, Ehleringer JR (2004) Expressing leaf water and cellulose oxygen isotope ratios as enrichment above source water reveals evidence of a Pecllet effect. *Oecologia* 138:426–435
- Belmecheri S, Wright WE, Szejner P, Morino KA, Monson RK (2018) Carbon and oxygen isotope fractionations in tree rings reveal interactions between cambial phenology and seasonal climate. *Plant, Cell Environ* 41:2758–2772
- Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ (2015) Larger trees suffer most during drought in forests worldwide. *Nature Plants* 1(10):15139
- Bentz BJ, Regniere J, Fettig CJ, Hansen M, Hayes JL, Hicke JA, Kelsey RG, Negron JF, Seybold SJ (2010) Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. *Science* 60:602–613
- Bracewell RR, Six DL (2014) Breadscape specificity in a bark beetle-fungal symbiosis: a spatio-temporal analysis of the mycangial fungi of the western pine beetle. *MicrobEcol* 68:859–870
- Briffa KR, Melvin TM (2011) A closer look at regional curve standardization of tree-ring records: justification of the need, a warning of some pitfalls, and suggested improvements in its application. In: Hughes MK, Diaz HF, Swetnam TW (eds) *Dendroclimatology*. Springer, Dordrecht, pp 113–145
- Churchill DJ, Larson AJ, Dahlgreen MC, Franklin JF, Hessburg PF, Lutz JA (2013) Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. *For Ecol Manage* 291:442–457
- Cook ER, Krusic PJ (2014) ARSTAN version 44h3: A tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics. Tree-Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University, Palisades, New York, USA
- Cook BI, Mankin JS, Marvel K, Williams AP, Smerdon JE, Anchukaitis KJ (2020) Twenty-first century drought projections in the CMIP6 forcing scenarios. *Earth's Future* 8(6)
- Cooper LA, Reed CC, Ballantyne AP (2018) Mountain pine beetle attack faster growing lodgepole pine at low elevations in western Montana, USA. *For Ecol Manage* 427:200–207
- Coops NC, Waring RH, Wulder MA, White JC (2009) Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. *Remote Sens Environ* 113:1058–1066
- Craighead FC (1925) The dendroctonus problem. *J Forest* 23:340–354
- Dancho M, Vaughan D (2018) Tidyquant: Tidy quantitative financial analysis. <https://bit.ly/2KuBP98>
- Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable isotopes in plant ecology. *Annu Rev Ecol Syst* 33:507–559
- De la Mata R, Hood S, Sala A (2017) Insect outbreak shifts the direction of selection from fast to slow growth rates in the long-lived conifer *Pinus ponderosa*. *Proc Natl Acad Sci* 114:7391–7396
- DeMars Jr. CJ, Roettgering BH (1982) Western pine beetle. Forest insect and disease Leaflet 1. USDA forest service, Washington DC, USA
- Edwards TWD, Fritz P (1986) Assessing meteoric water composition and relative humidity from ^{18}O and ^2H in wood cellulose: paleoclimatic implications for southern Ontario. *Canada Appl Geochem* 1(6):715–723
- Ehleringer JR, Hall AE, Farquhar GD (eds) (1993) Stable isotopes and plant carbon-water relations. Academic Press, New York
- Eldardiry H, Mahmood A, Chen X, Hossain F, Nijssen B, Lettenmaier DP (2019) atmospheric river-induced precipitation and snowpack during the Western United States Cold Season. *J Hydrometeorol* 20:613–630
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Funct Plant Biol* 9(2):121–137
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537
- Farquhar GD, Lloyd J (1993) Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial plants and the

- atmosphere. In: Ehleringer JR, Hall AE, Farquhar GD (eds) Stable isotopes and plant carbon-water relations. Academic Press, San Diego, pp 47–70
- Ferrell RM (2017) Patterns of above-ground ecosystem interactions of regolith in the southern Sierra Nevada of California. Master's thesis, University of California, Davis, CA, USA
- Ferrenberg S, Kane JM, Mitton JB (2014) Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia* 174(4):1283–1292
- Fettig CJ, Mortenson LA, Bulaon BM, Foulk PB (2019) Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. For *Ecol Manage* 432:164–178
- Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yezpe EA, Macalady AK, Pangle RE, McDowell NG (2013) Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytol* 198:567–578
- Gaylord ML, Kolb TE, McDowell NG (2015) Mechanisms of piñon pine mortality after severe drought: a retrospective study of mature trees. *Tree Physiol* 35(8):806–816. <https://doi.org/10.1093/treephys/tpv038>
- Gleick PH (1987) Regional hydrologic consequences of increases in atmospheric CO₂ and other trace gases. *Clim Change* 10:137–160
- Goulden ML, Anderson RG, Bales RC, Kelly AE, Meadows M, Winston GC (2012) Evapotranspiration along an elevation gradient in the Sierra Nevada. *J Geophys Res* 117:G03028
- Graf M, Reid ML, Aukema BH, Lindgren BS (2012) Association of tree diameter with body size and lipid content of mountain pine beetles. *Can Entomol* 144:467–477
- Griffin D, Anchukaitis KJ (2014) How unusual is the 2012–2014 California drought? *Geophys Res Lett* 41(24):9017–9023
- Guerrieri R, Belmecheri S, Ollinger SV, Asbjornsen H, Jennings K, Xiao J, Stocker BD, Martin M, Hollinger DY, Bracho-Garrillo R, Clark K (2019) Disentangling the role of photosynthesis and stomatal conductance on rising forest water-use efficiency. *Proc Natl Acad Sci* 116(34):16909–16914
- Helama S, Lindholm M, Timonen M, Eronen M (2004) Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods. *Theoret Appl Climatol* 79(3–4):239–254
- Hessburg PF, Spies TA, Perry DA, Skinner CN, Taylor AH, Brown PM, Stephens SL, Larson AJ, Churchill DJ, Povak NA, Singleton PH (2016) Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. For *Ecol Manage* 366:221–250
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree Ring Bull* 43:69–78
- Hood S, Sala A (2015) Ponderosa pine resin defenses and growth: metrics matter. *Tree Physiol* 35:1223–1235
- Hood S, Sala A, Heyerdahl EK, Boutin M (2015) Low-severity fire increases tree defense against bark beetle attacks. *Ecology* 96(7):1846–1855
- Hood SM, Baker S, Sala A (2016) Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. *Ecol Appl* 0:1–17
- Jones J (2015) California's most significant droughts: comparing historical and recent conditions. California Department of Water Resources, Sacramento
- Kane JM, Kolb TE (2010) Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Physiol Ecol* 161:601–609
- Keen RK (2019) Using tree-ring growth and stable isotopes to explore ponderosa pine ecophysiological responses to climate variability and the 2012–2015 California Drought. Master's thesis, Utah State University, Logan, UT, USA
- Kerhoulas LP, Kolb TE, Koch GW (2013) Tree size, stand density, and the source of water used across seasons by ponderosa pine in northern Arizona. For *Ecol Manage* 289:425–433
- Kichas NE, Hood SM, Pederson GT, Everett RG, McWethy DB (2020) Whitebark pine (*Pinus albicaulis*) growth and defense in response to mountain pine beetle outbreaks. For *Ecol Manage* 457:117736
- Knapp PA, Soule PT, Maxwell JT (2013) Mountain pine beetle selectivity in old-growth ponderosa pine forests, Montana, USA. *Ecol Evol* 3:1141–1148
- Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Steward JE, Weed AS (2016a) Observed and anticipated impacts of drought on forest insects and diseases in the United States. For *Ecol Manage* 380:321–334
- Kolb TE, Grady KC, McEtrick MP, Herrero A (2016b) Local-scale drought adaptation of ponderosa pine seedlings at habitat ecotones. For *Sci* 62(6):641–651
- Kolb TE, Keefover-Ring K, Burr SJ, Hofstetter R, Gaylord M, Raffa KF (2019) Drought-mediated changes in tree physiological processes weaken tree defenses to bark beetle attack. *J Chem Ecol* 45(10):888–900
- Krannitz PG, Duralia TE (2004) Cone and seed production in *Pinus ponderosa*: a review. *Western North America Naturalist* 208–218
- Larson DR, Hann DW (1985) Equations for predicting diameter and squared diameter inside bark at breast height for six major conifers of southwest Oregon. Research Note 77. Forest Research Laboratory, Corvallis, OR, USA
- Laumer W, Andreu L, Helle G, Schleser GH, Wieloch T, Wissel H (2009) A novel approach for the homogenization of cellulose to use micro-amounts for stable isotope analysis. *Rapid Commun Mass Spectrom* 23:1934–1940
- Leavitt SW, Danzer SR (1993) Method for batch processing small wood samples to holocellulose for stable isotope analysis. *Anal Chem* 65:87–89
- Leavitt SW, Woodhouse CA, Castro CL, Wright WE, Meko DM, Touchan R, Griffin D, Ciancarelli B (2011) The North American monsoon in the US Southwest: potential for investigation with tree-ring carbon isotopes. *Quatern Int* 235:101–107
- Margoles DS (2011) Mountain pine beetle-Whitebark pine dynamics in a subalpine ecosystem of the Pioneer mountains, southwest Montana. Master's thesis. University of Minnesota, Minneapolis, MN, USA
- McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. *Quatern Sci Rev* 23:771–801
- McDonald PM (1983) Local volume tables for Pacific madrone, tanoak, and California black oak in north-central California. Research Note PSW-362. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, USA
- McDowell M, Brooks JR, Fitzgerald SA, Bond BA (2003) Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant Cell Environ* 226:631–644
- McDowell NG, Adams HD, Bailey JD, Kolb TE (2007) The role of stand density on growth efficiency, leaf area index, and resin flow in southwestern ponderosa pine forests. *Can J For Res* 37:343–355
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M (2011) The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol Evol* 26:523–532
- McLaughlin BC, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson SE (2017) Hydrologic refugia, plants, and climate change. *Glob Change Biol* 23:2941–2961
- Miller JM, Keen FP (1960) Biology and control of the western pine beetle: a summary of the first fifty years of research. USDA, Washington

- Moore J, McAfee L, Jirka A, Heath Z, Smith B (2017) 2016 Aerial Survey Results California. Research Paper R5-Pr-034. USDA Forest Service, Pacific Southwest Region, USA
- Moreira X, Mooney KA, Rasmann S, Petry WK, Carrillo-Gavilán A, Zas R, Sampedro L (2014) Trade-offs between constitutive and induced defenses drive geographical and climatic clines in pine chemical defenses. *Ecol Lett* 17:537–546
- Mote PW, Hamlet AF, Clark MP, Lettenmaier DP (2005) Declining mountain snowpack in western North America. *Bull Am Meteor Soc* 86:39–50
- North M, Hurteau M, Fiegenger R, Barbour M (2005) Influence of fire and El Niño on tree recruitment by species in Sierran mixed conifer. *For Sci* 51:187–197
- Parsons DJ, DeBenedetti SH (1979) Impact of fire suppression on a mixed-conifer forest. *For Ecol Manage* 2:21–33
- Person HL (1928) Tree selection by the western pine beetle. *J Forest* 26:564–578
- Pile LS, Meyer MD, Rojas R, Roe O, Smith MT (2019) Drought impacts and compounding mortality of forest trees in the southern Sierra Nevada. *Forests* 10:237
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2015) nlme: linear and nonlinear mixed effects models. R package version 3.1–121. <https://CRAN.R-project.org/package=nlme>
- Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecol Monogr* 53:27–49
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58:501–517
- Rigling A, Brühlhart H, Bräker OU, Forster T, Schweingruber FH (2003) Effects of irrigation on diameter growth and vertical resin duct production in *Pinus sylvestris* L. on dry sites in the central Alps Switzerland. *For Ecol Manage* 175(1–3):285–296
- Rinne KT, Boettger T, Loader NJ, Robertson I, Switsure VR, Waterhouse JS (2005) On the purification of α -cellulose from resinous wood for stable isotope (H, C and O) analysis. *Chem Geol* 222:75–82
- Roden J (2008) Cross-dating of tree ring $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ time series. *Chem Geol* 252:72–79
- Roden JS, Ehleringer LG, JR, (2000) A mechanistic model for interpretation of hydrogen and oxygen isotope ratios in tree-ring cellulose. *Geochimica et Cosmochimica Acta* 64:21–35
- Roden JS, Ehleringer JR (2007) Summer precipitation influences the stable oxygen and carbon isotopic composition of tree-ring cellulose in *Pinus ponderosa*. *Tree Physiol* 27:491–501
- Sevanto S, McDowell NG, Dickman LT, Pangle R, Pockman WT (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypothesis. *Plant Cell Environ* 37:153–161
- Smith GI, Friedman I, Klieforth H, Hardcastle K (1979) Areal distribution of deuterium in eastern California precipitation, 1968–1969. *J Appl Meteorol* 18:172–188
- Stamp N (2003) Out of the quagmire of plant defense hypothesis. *Q Rev Biol* 78:23–55
- Stephens SL, Lydersen JM, Collins BM, Fry DL, Meyer MD (2015) Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. *Ecosphere* 6(5):1–63
- Stephenson NL, Das AJ, Ampersee NJ, Bulaon BM, Yee JL (2019) Which trees die during drought? The key role of insect host-tree selection. *J Ecol* 107(5):2383–2401
- Stewart IT, Cayan DR, Dettinger MD (2004) Changes in snowmelt run-off timing in western North America under a business as usual climate change scenario. *Clim Change* 62:217–232
- Stokes MA, Smiley T (1968) An introduction to tree-ring dating. University of Chicago Press, Chicago
- Stovall AE, Shugart H, Yang X (2019) Tree height explains mortality risk during an intense drought. *Nat Commun* 10(1):1–6
- Szejner P, Wright WE, Babst F, Belmecheri S, Trouet V, Leavitt SW, Ehleringer JR, Monson RK (2016) Latitudinal gradients in tree-ring stable carbon and oxygen isotopes reveal differential climate influences of the North American Monsoon system. *J Geophys Res* 121:1978–1991
- Ulrich DE, Still C, Brooks JR, Kim Y, Meinzer FC (2019) Investigating old-growth ponderosa pine physiology using tree-rings, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and a process-based model. *Ecology* 100:e02656
- Van de Water KM, Safford HD (2011) A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecol* 7:26–58
- Van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT (2009) Widespread increase of tree mortality rates in the Western United States. *Science* 323:521–524
- Voelker SL (2011) Age-dependent changes in environmental influences on tree growth and their implications for forest responses to climate change. In: Meinzer FC, Lachenbruch B, Dawson TE (eds) Size and age-related changes in tree structure and function. Springer, New York, pp 455–479
- Voelker SL, Meinzer FC, Lachenbruch B, Brooks JR, Guyette RP (2014) Drivers of radial growth and carbon isotope discrimination of bur oak (*Quercus macrocarpa* Michx.) across continental gradients in precipitation, vapour pressure deficit and irradiance. *Plant Cell Environ* 37(3):766–779
- Voelker SL, Merschel AG, Meinzer FC, Ulrich DEM, Spies TA, Still CJ (2019) Fire deficits have increased drought-sensitivity in dry conifer forests: fire frequency and tree-ring carbon isotope evidence from Central Oregon. *Glob Change Biol* 25:1247–1262
- Waring RH, Pitman GB (1985) Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66:889–897
- Williams AP, Allen CD, Millar CI, Swetnam TW, Michaelsen J, Still CJ, Leavitt SW (2010) Forest responses to increasing aridity and warmth in the southwestern United States. *Proc Natl Acad Sci* 107(50):21298–21294
- Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD, Dean JS, Cook ER, Gangadagamage C, Cai M, McDowell NG (2012) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat Clim Change* 3:292–297
- Williams AP, Cook ER, Smerdon JE, Cook BI, Abatzoglou JT, Bolles K, Baek SH, Badger AM, Livneh B (2020) Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* 368(6488):314–318
- Wise EK, Dannenberg MP (2017) Reconstructed storm tracks reveal three centuries of changing moisture delivery to North America. *Sci Adv* 3:e1602263
- Yanchuk AD, Murphy JF, Wallin KF (2008) Evaluation of genetic variation of attack and resistance in lodgepole pine in the early stages of a mountain pine beetle outbreak. *Tree Genet Genomes* 4:171–180