



Variable climate response differentiates the growth of Sky Island Ponderosa Pines

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Abstract

Key message The seasonally cool and moist conditions of spring improved the growth of two co-occurring ponderosa pine species, which displayed different seasonal climatic responses and length of correlations to drought.

Abstract We examined the climatic sensitivity of two partially sympatric pine species growing at their transition zone in the Santa Catalina Mountains, AZ, USA. *Pinus arizonica* is found at lower elevations compared to *P. ponderosa* var. *brachyptera*. Ring widths were measured in trees at two sites and correlated with precipitation, temperature, and Palmer Drought Severity Index to assess the influence of climate on growth. The two species were analyzed within and between sites, which have similar elevation, aspect, and species composition, although soils at the two sites have different water-holding capacities. Response function analyses of *P. arizonica* [sampled near its upper (and wetter) elevation limit], and *P. ponderosa* var. *brachyptera* [sampled near its lower (and drier) elevation limit] indicated that annual growth correlated positively and strongly with spring precipitation at both study locations. Local site conditions had a major impact on tree growth and variability in site conditions helped resolve the differences in species' response to climate. For example, at the less dry site, growth of the lower-elevation pine (*P. arizonica*) responded to early-winter precipitation, while *P. ponderosa* var. *brachyptera* did not. Also, correlation analysis indicated that *P. arizonica*'s growth was more sensitive to drought for longer periods than *P. ponderosa* var. *brachyptera*. Finally, partial temperature-growth correlations of *P. arizonica* and *P. ponderosa* var. *brachyptera* indicated growth was limited by increased growing season and winter respiration, respectively. Rising night-time temperatures during spring significantly reduced growth of *P. arizonica* at Mt. Lemmon. These findings demonstrate subtle yet meaningful interspecies differences in sensitivity to seasonal moisture stress and use of carbon resources.

Keywords Dendroecology · Drought stress · Pinaceae · Response function · Tree ring · *Ponderosae*

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Introduction

The Santa Catalina Mountains, near Tucson, Arizona, USA, are among the best-known and well-studied Madrean Sky Islands, which are high-elevation mountains defined by pine-oak forests (Shreve 1915, 1917, 1919; Whittaker and Niering 1965, 1975; Whittaker et al. 1968; Bezy 2016). Two partially sympatric pine species grow at the higher elevations: *Pinus arizonica* Engelm. and *P. ponderosa* var. *brachyptera* (Engelm.) Lemmon, a closely related variety of *P. ponderosa* [and previously misidentified as *P. ponderosa* var. *scopulorum* (Engelm.)], also known as Taxon X (Rehfeldt 1999; Epperson et al. 2009; Willyard et al. 2017).

Pinus arizonica and *P. ponderosa* var. *brachyptera*, Diploxylon pines of the subsection *Ponderosae*, are large trees that grow throughout the mountainous and semiarid

regions of the southwestern United States (Perry 1991; Farjon and Styles 1997; Price et al. 1998). *P. ponderosa* var. *brachyptera*, comprising three-needle and mixed-needle morphotypes, survive exclusively at the highest elevations (2300–3000 m) and in cold air drainages (Rehfeldt 1999; Epperson et al. 2001), while the five-needle *P. arizonica* is found at lower elevations (1800–2600 m), and is considered part of the ponderosa pine complex. As mean annual precipitation increases with elevation from orographic processes (Sheppard et al. 2002), *P. arizonica* is more successful at surviving in warmer and drier habitats, whereas *P. ponderosa* var. *brachyptera* survives in cooler and wetter habitats. *P. arizonica* extends from southeastern Arizona and southwestern New Mexico to the Sierra Madre of northern Mexico (Perry 1991). In comparison, *P. ponderosa* var. *brachyptera* ranges from northern Nevada to southern Texas (USDA, NRCS 2017). On south-facing slopes of the Santa Catalina Mountains, shallow soils are mostly homogeneous lithosols of low water-holding capacity that could promote moisture limitations on annual growth (Shreve 1915, 1919; Whittaker and Niering 1965; Whittaker et al. 1968; Bezy 2016). The transitions in taxa on south slopes are quite dramatic occurring over 100 m horizontal distance (Epperson et al. 2001).

Evaluating geographic variation in locally adapted populations helped determine differences in species' growth responses to climate throughout their range (Norris et al. 2006; Shinneman et al. 2016; McCullough et al. 2017). Although previous studies indicate North American pine growth is influenced primarily by seasonal precipitation (Dodge 1963; Fritts et al. 1965; Fritts 1976; Norris et al. 2006; Griffin et al. 2013; Dannenberg and Wise 2016; Shinneman et al. 2016; González-Cásares et al. 2017), few ecological studies have compared morphologically distinct taxa to identify interspecific differences (Haller 1965; Pelouquin 1984; Rehfeldt 1993; Epperson et al. 2001).

Our study design allowed us to identify individual taxa in the field and evaluate differential sensitivity to climate and water stress. This was accomplished by correlating seasonal climate data with widths of annual tree rings collected from transition zones where both taxa were present. Taxonomic relationships were determined by estimating (from a small number of branchlets) the frequency of needles per fascicle, an easy way to identify traits in the field and useful for characterizing populations (Epperson et al. 2001). We sampled ring widths to provide information on the climatic factors limiting growth from trees sampled under environmental stress, which occurs near the lower and upper limits of species distributions (Lamarche and Stockton 1974). The growth of trees in this semiarid region is primarily limited by water stress rather than temperature (Fritts 1976). Under low-moisture conditions, individual trees produce rings that are very narrow.

Adapted to different ecological conditions, *P. arizonica* and *P. ponderosa* var. *brachyptera* are high-elevation tree species that express dissimilar tolerances to water shortage through their growth responses. Projected climate warming in these semiarid mountainous regions could reduce tree growth as increasing temperatures and decreasing precipitation elevate moisture stress (Barichivich et al. 2014). We expect water stress to be greatest at a tree's lower elevational limit where soil moisture available for growth is lowest (Sheppard et al. 2002). Thus, at the transition zone where the two species co-occur, our first hypothesis predicts *P. ponderosa* var. *brachyptera* growing at its lower-warm elevational limit to be more sensitive to dry conditions and changes in temperature than *P. arizonica* growing near its upper cool-moist elevational limit (Lamarche and Stockton 1974; Adams and Kolb 2005). Palmer Drought Severity Index (PDSI; a measure of soil moisture availability), was evaluated in a second hypothesis predicting that positive growth-PDSI correlations would differ between taxa. The premise is that trees originating from moist (*P. ponderosa* var. *brachyptera*) compared to dry (*P. arizonica*) environments would be more susceptible to moisture stress.

Methods

Study area and sampling

The study areas of Mt. Lemmon (MTL; 32.443°_N, –110.788°_W) and Mt. Bigelow (BIG; 32.414°_N, –110.715°_W) are located within the Santa Catalina Mountains (2,500 m a.s.l.) of the Coronado National Forest, approximately 28 km straight-line distance northeast of Tucson, Arizona, Pima County, USA (Fig. 1). The ponderosa pine species were sampled from steep slopes [average gradient of 45% (MTL) and 37% (BIG); data not shown], of Lithic Haplustolls (Buol 1966; Brown 1968) derived from granite and gneiss, gravely to rocky in texture and shallow in depth (*c.* 50–140 cm; data not shown); a frigid complex with average available water-holding capacity (AWHC) of 9.2% for MTL and 3.8% for BIG (Suppl. Figure 1). The mixed conifer forest comprises *P. arizonica*, *P. ponderosa* var. *brachyptera*, *P. strobiformis*, *Pseudotsuga menziesii*, *Quercus hypoleucoides*, *Q. gambelii*, *Q. reticulata* (Brown 1968), and rarely *Abies concolor*. Half of the annual precipitation falls during the summer monsoon (July through September; JAS). Winter storms (November through March: NDJFM) provide an additional third or more of the annual rainfall (Table 2; Sheppard et al. 2002).

Ponderosa pine species were identified in the field by conducting average needle counts (*c.* ≥ 10 fascicles). Trees with average needle numbers per fascicle < 4.6 and ≥ 4.6 were designated *P. ponderosa* var. *brachyptera* and *P. arizonica*, respectively (Haller 1965; Pelouquin 1984). While

Fig. 1 Locations of two study sites sampled for tree-ring analysis: MTL (Mt. Lemmon) and BIG (Mt. Bigelow). Black triangles mark the study sites northeast of Tucson, AZ, USA

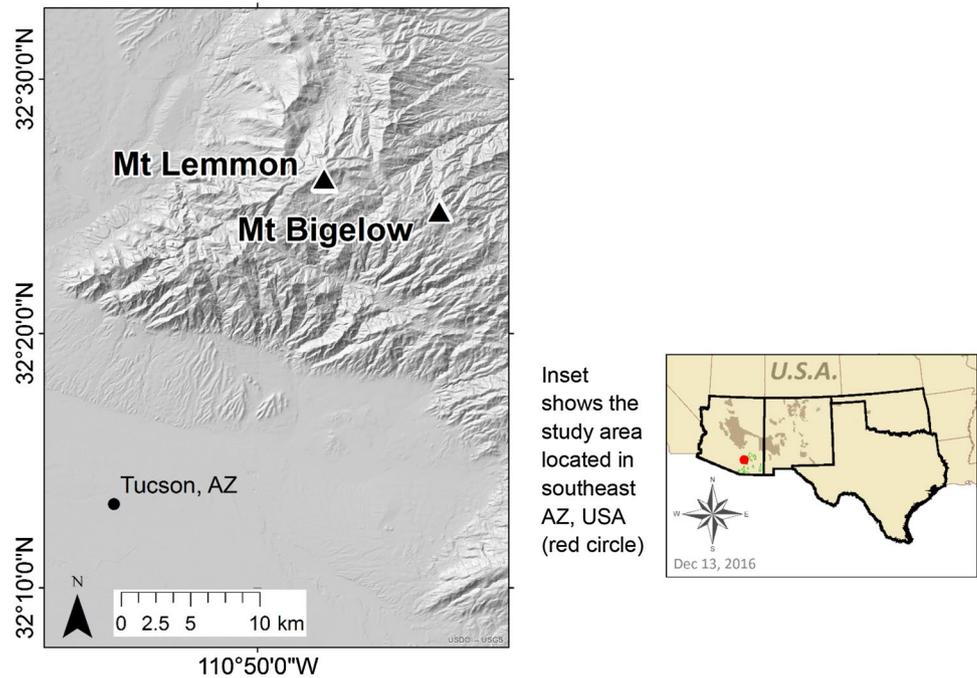


Table 1 Sampling design used for two south-facing slopes, Santa Catalina range (sites MTL and BIG)

PPB	PPB	PPB	PPB	PPB
PPB	PPB	PPB	PPB	PPB
PPB	PPB	PPB	PPB	PPB
PPB/PAZ	PPB/PAZ	PPB/PAZ	PPB/PAZ	PPB/PAZ
PPB/PAZ	PPB/PAZ	PPB/PAZ	PPB/PAZ	PPB/PAZ
PPB/PAZ	PPB/PAZ	PPB/PAZ	PPB/PAZ	PPB/PAZ
PAZ	PAZ	PAZ	PAZ	PAZ
PAZ	PAZ	PAZ	PAZ	PAZ
PAZ	PAZ	PAZ	PAZ	PAZ

Elevation increases from the bottom to top of schematic. Each box represents 1 sample point on a 5×9 grid. One tree was sampled *c.* every 10 m except for the center of the transition zone, where 1 PPB and 1 PAZ each were sampled

N = 30 trees collected per species

PAZP. *arizonica*, PPB *P. ponderosa* var. *brachyptera*

avoiding ridges and cold air drainages, we sampled transition zones within the lower and upper moisture availability limits, respectively, for *P. ponderosa* var. *brachyptera*, and *P. arizonica*. Nine horizontal transects were established at each study area (MTL and BIG) on southern aspects of similar slope. The nine transects were equivalent to a 5×9 grid with 10-m spacing. The nearest tree was sampled to each point, except for the middle of the transition zone (i.e., the three innermost transects), where one *P. ponderosa* var. *brachyptera* and one *P. arizonica* were sampled (Table 1). From 2010 to 2012 all healthy trees ≥ 8 cm diameter at breast height (DBH) were selected and sampled. Individual

sample trees were tagged and mapped using North American Datum of 1983 (NAD83) geographic coordinates obtained through global positional system (GPS) data collected at the field plots (*n* = 120; i.e., 2 sites × 2 species × 30 trees). Two or more tree-core samples were collected from each tree using a 5.5-mm increment borer, dried and glued in wood core mounts, and sanded to 600 grit to visualize clear ring boundaries. We visually crossdated all samples using the skeleton-plot technique (Stokes and Smiley 1996). Tree-ring widths were measured to the nearest 0.01 mm using scanned images (2400 dpi resolution) and CooRecorder™ software (Cybis Elektronik 2010). Accurate calendar dates were assigned to each ring in the time sequence with CDendro™ software (Cybis Elektronik 2010). Sample dating was statistically verified with the program COFECHA (Holmes et al. 1986).

Climate data

Specific climate data sets for MTL and BIG were developed with 1-km resolution using the ANUSPLIN package (Hutchinson and Xu 2013) by creating 1925–2009 estimates of the temperature and precipitation variables (McKenney et al. 2011). Similarly, the 4-km gridded PDSI values obtained from the West Wide Drought Tracker website (Abatzoglou et al. 2017) were used to create estimates of the local PDSI variable (model and website development by the University of Idaho and the Desert Research Institute, Reno, Nevada). The composite PDSI index is based on variation in temperature, precipitation, and the local AWHC of the soil, and quantifies longer term departures from normal

moisture patterns; more negative values indicate drought stress, ranging from ≤ -4 for extremely dry conditions to $\geq +4$ for extremely wet conditions (Palmer 1965). Climatic variables were summarized as monthly values of average temperature (T_{AVG}), average minimum temperature (T_{MIN}), average maximum temperature (T_{MAX}), total precipitation (PCP), and average PDSI. To validate the quality of climate data, we conducted correlation analysis using `cor` function in R (R Core Team 2016) with local datasets and displayed a matrix of correlation coefficients created using the `corrplot` package (Wei and Simko 2017). Correlation was also used to examine the interrelationship between climate variables at both sites (“Appendix 1”).

Trend and climate-growth analysis

Juvenile growth trends were removed from the average ring-width series of individual trees (i.e., de-trended) by fitting a modified negative exponential curve to create standardized indices using the ARSTAN program (Cook 1985). Autocorrelation arises from the persistence of climatic effects on tree growth, which was removed by autoregressive modeling (Cook 1985). The final master ARSTAN chronology was created using a bi-weight robust mean to account for climatic variance and endogenous disturbance (Cook 1985). We calculated the descriptive statistics of running RBar, expressed population signal (EPS), signal-to-noise ratio (SNR), mean sensitivity (MS), Gini coefficient (G), standard deviation (SD), and autocorrelation (AC) using the `dpIR` package (Bunn 2008, 2010) for R, which was also used to plot the ARSTAN chronologies. Smoothing splines were applied to the chronologies with defaults in `dpIR`. All other tree-ring statistics were obtained directly from the ARSTAN DOS output files (Cook 1985). The running RBar [i.e., between-tree correlation (Rbt)] is the average correlation coefficient between all possible pairs of indexed series drawn from different trees (Wigley et al. 1984; Briffa and Jones 1990); we chose a 40-year moving window with 20-year overlap. The coefficient of variation (CV) of Rbt was expressed as the SD of the mean for all species and sites combined. EPS measures the common variability of a chronology when series are averaged, ranging from 0 to 1, and a value greater than 0.85 indicates a strong common signal of the chronology (Wigley et al. 1984; Briffa and Jones 1990; Speer 2010). SNR in de-trended tree-ring series is the ratio of two variances (common climate signal and random error). Mean sensitivity measures the relative change in ring widths from year-to-year (Fritts 1976). It theoretically ranges from 0 (all rings have same width) to 2 (locally absent ring every other year), but in practice varies from 0.1 to 0.6 (Biondi and Qeadan 2008). Gini coefficient ranges from 0 to 1, measures diversity in tree-ring chronologies regardless of the degree of autocorrelation, and improves on intra-annual variability

comparisons among species and sites (Bunn et al. 2013; DeRose et al. 2015).

Because monthly climate variables are often highly inter-correlated, tree-ring analyses were conducted using both partial correlations (Meko et al. 2011) and regression involving principal components (Fritts 1974). Partial correlations address collinearity of the primary and secondary climate variables prior to summarizing the seasonal climate signal in the tree-ring data. Partial correlations were used to compare each residual plot chronology to monthly climatic variables to test the null hypothesis of no effects ($r=0$; $\alpha \leq 0.05$). Pearson correlation coefficients were calculated for the primary climate variable (PCP summed; or PDSI averaged), and partial correlations were computed for the secondary climate variable (T_{AVG}), independent of the variance related to the primary variable. Climate variables (PCP, T_{AVG} , and PDSI) were tested over a 14-month climate window from the preceding August to September of the current growth year, to account for the influence of prior environmental conditions on the current season’s growth. Subsequently, maximum climate–growth correlations were determined across season lengths of 1, 3, and 6 months reflecting seasonal fluctuations of PCP (primary) and T_{AVG} (secondary) climate variables. Season lengths of 1, 3, 6, 12, and 20 months determined the maximum influence of PDSI (primary) and T_{AVG} (secondary) variables on climate–growth correlations over a time window from the previous October to current August. All seasonal correlations were completed with the `treeclim` package (Zang et al. 2015) for R, using the ‘`seascorr`’ function. Finally, we quantified the effect size of PDSI using Pearson correlation coefficients (r) for single months using `cor` function in R.

We investigated significant variables ($p \leq 0.05$) identified by simple correlation analysis (`treeclim` package; Zang et al. 2015), which were consistent in sign and magnitude, as potential predictors to include in response function analysis. Fritts (1974) introduced regression involving principal components to address multicollinearity by transforming predictor climate variables to produce a set of uncorrelated data points. The calculation of the response function regresses tree-ring data against transformed monthly climatic variables to select the parameters that influence tree growth (Fritts 1974, 1976). Each principal component variable explains partial variance in the data set. Relationships between climatic variables and ring-width indices were examined using multivariate estimates obtained from the principal component regression model. The analysis computed bootstrapped response functions using the `treeclim` package (Zang et al. 2015). To obtain robust parameter estimates, we used bootstrapping to test regression coefficients and the stability of estimates (Guiot 1991). Twenty-eight monthly climatic variables (i.e., 14 PCP + 14 T_{MIN}) were analyzed from July through December of the previous year

(excluding the transition month of October), and January through September of the current year. Climate variables were partitioned into seasons to quantify water balance (i.e., PDSI), precipitation, and temperature effects during key periods in our study plots (winter, spring and summer). Seasonal variables were derived by combining the monthly data into two rainy seasons consisting of 3 and 5 months respectively: summer (JAS) and winter (NDJFM) separated by 3 months of arid spring (AMJ). Summer season spanned the months from previous July to previous September, and current July to current September; winter season spanned the months from previous November to the current March, and arid spring spanned the months from current April to current June. Climate was also divided into four seasons of 3 months each, which partitioned winter into fall (OND) and winter (JFM). Mean chronologies and correlation bar graphs were plotted using plotting functions in the dplR package; all other plots were created using standard R plotting functions. Seasonal variables were tested for departure from normality with the Kolmogorov–Smirnov test ($\alpha=0.05$). Normality tests, and distributions of single variables were analyzed using JMP Pro, v 13.0 (Copyright© 2016 SAS Institute Inc., Cary, NC, USA), or Sigma Plot, v 13.0 (Copyright© 2014 Systat Software, Inc., San Jose, CA, USA).

Results

Annual and monthly climate

Climate data of the two sites were averaged to obtain a summary record for the Santa Catalina Mountains. Over the 84-year study period (1925–2009), average yearly PCP is 681.1 ± 163.9 mm and average yearly T_{AVG} is 10.9 ± 0.5 °C (Table 2). Multicollinearity between PCP and T_{AVG} is low, but significant, with negative correlations of $r = -0.3$ (Prob > |pI| = 0.005; Zar 2010). The average PDSI broadly ranges between ± 4.0 with a few values from 5.0 to 7.0 (Suppl. Figure 3). We identified four dry periods (PDSI < -2.0) at both sites of two or more year's duration: 1936–1939; 1947–1948; 2002–2003; 2006–2007.

Seasonal climate

PCP was evenly distributed between two rainy seasons: summer (JAS; average 299 ± 73.3 mm) and winter (NDJFM; average 299.2 ± 155.0 mm), with August being the wettest month (Table 2; Suppl. Figure 4A). The driest season was spring (AMJ; average 48.3 ± 29.4 mm), with May being the driest month (median < 10 mm). Winter's median monthly T_{AVG} remained below 6.5 °C, with January being the coldest month (2.7 °C; Table 2; Suppl. Figure 4B). Summer remained above the median monthly T_{AVG} of 18.5 °C, with

Table 2 Summaries for climate data obtained from gridded data sets (McKenney et al. 2011) for two study sites: MTL and BIG

	MTL	BIG
Geographic coordinates, WGS84 (latitude, longitude)	32.43, -110.79	32.41, -110.71
Elevation (m)	2577	2534
Years spanned	1925–2009	1925–2009
Years of record	84	84
Yearly T_{AVG} (mean °C \pm SD)	11.0 ± 0.6	10.8 ± 0.5
January T_{AVG} (mean °C \pm SD)	2.8 ± 1.7	2.6 ± 1.8
July T_{AVG} (mean °C \pm SD)	19.5 ± 1.0	19.4 ± 0.8
Yearly PCP (mean mm \pm SD)	678.8 ± 164.1	685.0 ± 163.8
Winter PCP (mean mm \pm SD)	298.7 ± 154.5	299.7 ± 155.4
Arid spring PCP (mean mm \pm SD)	47.8 ± 29.2	48.8 ± 29.7
Summer PCP (mean mm \pm SD)	296.9 ± 72.9	301.1 ± 73.7

Temperature year considers coldest and hottest months: January and July. Precipitation year is divided into three seasons: winter (previous November–current March), arid spring (April–June), and summer (July–September)

July being the hottest month (19.5 °C). Spring (the driest season) saw the steepest increase in median T_{AVG} from 9 °C in April, to 18.5 °C in June (a rise of 9.5 °C; Suppl. Figure 4B).

Series length, chronology statistics, and growth patterns

Sawtimber trees > 25 cm diameter DBH were the predominant size class sampled at MTL with some pole-sized trees (10 to 25 cm); mean DBH (\pm SD) is 37.1 ± 14.4 cm, ranging from 15.5 to 85.3 cm. At BIG the sampled trees were smaller, including pole-sized and two saplings (5–10 cm); mean DBH (\pm SD) is 27.7 ± 13.2 cm, ranging from 7.7 to 61.2 cm. Although there were differences in average DBH between sites, the average series length (years \pm SD) and percentage of locally absent rings were similar between sites. Observed mean series length are 73 ± 23 years ranging from 35 to 148 years, and 76 ± 41 years ranging from 30 to 162 years, respectively for MTL and BIG. Locally absent rings accounted for 0.32% (MTL) and 0.24% (BIG) of the total rings in all series, combined.

The Gini coefficient and mean sensitivity index quantified moderate year-to-year differences that varied little between taxa or site (Table 3). In comparison, the indexed ring widths at MTL are significantly narrower for *P. arizonica* than *P. ponderosa* var. *brachyptera*, and *P. ponderosa* var. *brachyptera* exhibits the highest correlation in growth among trees (Rbt), higher SNR than *P. arizonica* at both sites, and significantly higher SD (14%) than *P. arizonica* at BIG, ($p < 0.05$; Table 3). Considering Rbt^2 , the coefficient

Table 3 General statistics for the common interval (1925–2009) of the de-trended chronologies for *P. arizonica* and *P. ponderosa* var. *brachyptera* from transition zones at two sites (MTL and BIG)

	MTL		BIG	
	<i>P. arizonica</i>	<i>Brachyptera</i>	<i>P. arizonica</i>	<i>Brachyptera</i>
No. trees (no. radii)	25 (58)	24 (64)	24 (40)	20 (40)
Ave no. \pm years SD	67 \pm 10	63 \pm 12	63 \pm 20	59 \pm 22
RWI	0.96a	1.00b	0.96	0.97
SD	0.38	0.36	0.40a	0.46b
MS	0.35	0.34	0.36	0.36
Gini	0.21	0.20	0.22	0.25
Rbt	0.35	0.39	0.33	0.40
Rbt ²	0.12	0.15	0.11	0.16
EPS	0.94	0.94	0.90	0.92
SNR	14.93	17.09	9.44	12.08
Autoregressive model	0	2	2	2
Variance due to autoregression	n.a.	16.4	23.4	28.7
AC1 ^a	0.13	0.32	0.38	0.45

Statistically significant differences are indicated by lowercase letters ($p < 0.05$)

RWI ring width index, SD standard deviation, MS mean sensitivity, Gini Gini coefficient, Rbt between-tree correlations, EPS expressed population signal, SNR signal-to-noise ratio, AC1 first-order autocorrelation

^aStandard chronology

of variation between species is 18% ($\bar{x} = 0.14$; $SD = 0.02$; Table 3). First-order autocorrelation values for the standard chronology are higher for BIG (0.41) on average than for MTL (0.22; Table 3).

Growth was reduced from the late 1930s to the late 1940s for *P. arizonica* and *P. ponderosa* var. *brachyptera* at BIG (Fig. 2c, d). A similar reduction in growth for the 1930s–1940s was not evident at MTL (Fig. 2a, b). The average growth of the two species was calculated to obtain indexed ring widths for BIG (0.70 ± 0.12), and MTL (0.91 ± 0.08) during seven drought years. The 7 years of decreased growth corresponded to low PDSI values recorded for 1936–1939 and 1946–1948 (Suppl. Figure 3). Average annual PDSI for the period was greater (wetter) at BIG (-2.15) than at MTL (-2.45). In contrast, the combined average index of annual rings measured at MTL (0.76 ± 0.23) during the latter 8-year dry period (2002–2009) is less than for BIG (0.90 ± 0.28). Average annual PDSI values were similar between sites for the 2002–2009 period (MTL, -2.39 ; BIG, -2.42).

Correlations

Simple correlation and response function

Correlation analysis (Suppl. Figure 5) identified seasonal variables for further response function analysis. Figure 3a shows significant positive growth responses with spring PCP (AMJ; $p < 0.05$) for both taxa, and the correlations were greater at MTL than at BIG. Figure 3a, b also show significant positive PCP-growth correlations for *P. arizonica*

at MTL during winter (ndJFM; $p < 0.05$), and early winter (ond; $p < 0.05$), and *P. arizonica*'s growth is negatively correlated with spring T_{MIN} (AMJ; Fig. 3A, $p < 0.05$)

PCP correlation and T_{AVG} partial correlation

Tree-ring index regressions with precipitation approach linearity, indicating they were not controlled by outliers (Suppl. Figure 6A–D; $p < 0.05$). Correlations between annual growth and single-month PCP for both species are positive and significant, increasing in strength when summing over multiple months (Fig. 4). The maximum positive PCP-growth correlations for *P. arizonica* occur for the 3-month periods ending in December, May, and June ($r \approx 0.4$) at MTL (Fig. 4a), and in June and July ($r \approx 0.4$) at BIG (Fig. 4b). For *P. ponderosa* var. *brachyptera*, maximum correlations occur for the 3-month periods ending in December ($r \approx 0.35$) and June ($r \approx 0.4$) at MTL (Fig. 4c), and in June and July at BIG ($r \approx 0.35, 0.4$, respectively; Fig. 4d). Partial correlations between annual growth and single-month T_{AVG} at MTL for *P. arizonica* and *P. ponderosa* var. *brachyptera* are negative and significant, increasing in strength when averaging over multiple months (Fig. 4a, c). The strongest partial correlations between growth and T_{AVG} for *P. arizonica* and *P. ponderosa* var. *brachyptera* occur for the 3-month period ending in July ($r \approx -0.30, -0.25$, respectively). Although the trend was largely negative, there are no significant negative partial correlations for *P. arizonica* at BIG (Fig. 4b), and the trend for *P. ponderosa* var. *brachyptera* is significant for the 3-month period ending in July ($r \approx -0.25$; Fig. 4d).

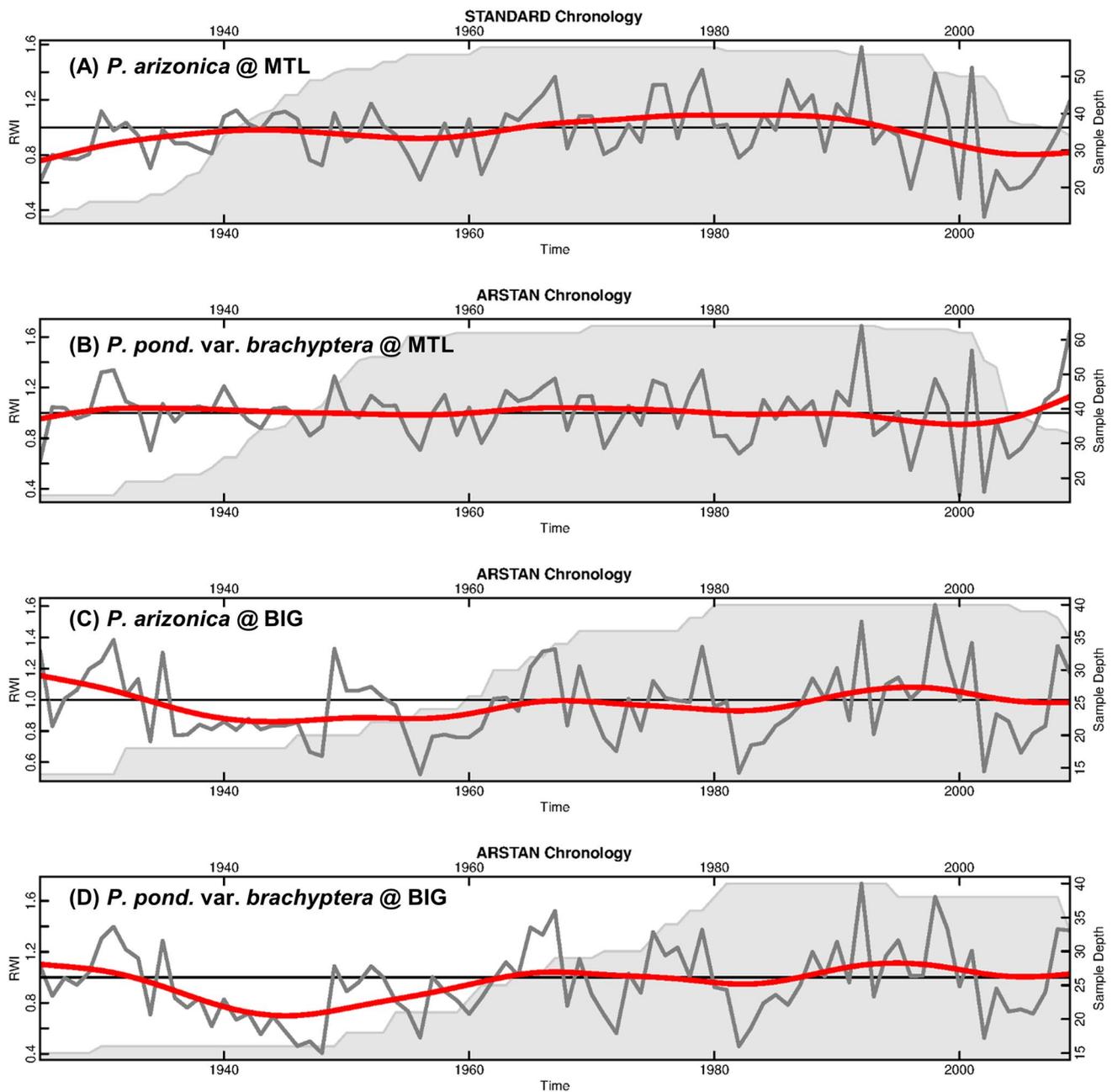


Fig. 2 ARSTAN or Standard chronologies of *P. arizonica* (a, c) and *P. ponderosa* var. *brachyptera* (b, d) when Expressed Population Signal (EPS) is greater than 0.85, and sample depth is > 14, for the refer-

ence period of 1925–2009. Two sites were evaluated: MTL (a, b) and BIG (c, d). The corresponding sample depth (number of tree cores) is indicated by shading

PDSI correlation and T_{AVG} partial correlation

Correlations between annual growth and single-month PDSI are positive and significant, with maximum values reached in July at both sites for *P. arizonica* [0.7 (MTL); 0.4 (BIG); Table 4a] and *P. ponderosa* var. *brachyptera* [0.5 (MTL); 0.4 (BIG); Table 4b]. Table 5 shows July's PDSI average effect size of 0.6 at MTL and 0.4 at BIG. Partial correlations between annual growth and single-month T_{AVG} are

negative but non-significant for both species at MTL (data not shown), increasing in strength, and becoming significant when averaging over multiple months (Fig. 5a, c). There are no significant temperature correlations for either species at BIG (Fig. 5b, d).

Correlations between annual growth and seasonal PDSI at MTL were of longer duration and stronger for *P. arizonica* (Table 4a) than *P. ponderosa* var. *brachyptera* (Table 4b). Significant positive correlations (r) range from $r \approx 0.3$ to

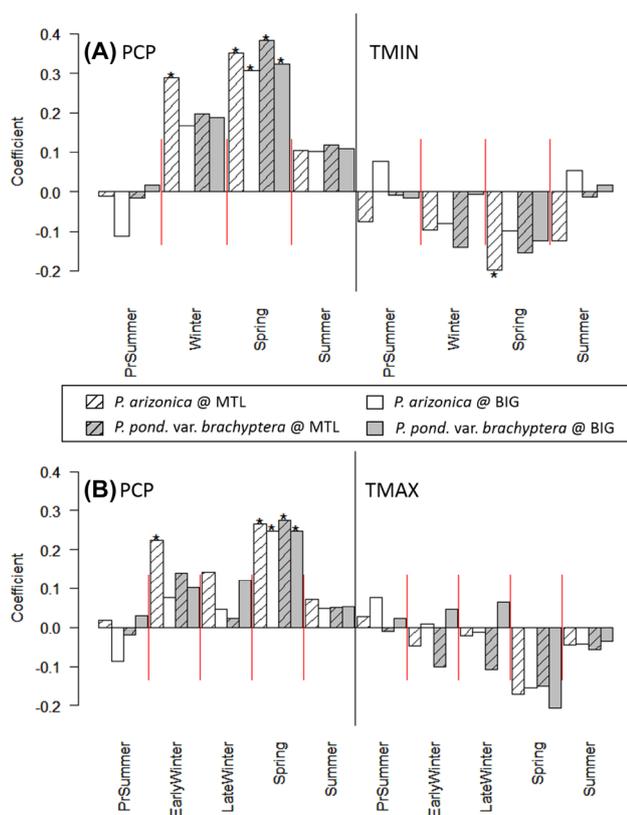


Fig. 3 Climate–growth relationships determined by principal components multiple regression for two species of ponderosa pine [*P. arizonica* = white, *P. ponderosa* var. *brachyptera* = grey] growing at two transition zones within the Santa Catalina Mountains: MTL (hatched bars) and BIG (non-hatched bars). Climate variables of precipitation (PCP) and minimum temperature (T_{MIN}) with seasons: Previous (Pr) Summer (July–September), Winter (November–March), Spring (April–June), and Summer (July–September) (a); and climate variables of PCP and maximum temperature (T_{MAX}) with 3-month seasons: Pr Summer, Early Winter (October–December), Late Winter (January–March), Spring, and Summer (b), which were related to the composite chronologies for the period of 1925–2009. The standard index was used in the growth analysis of *P. arizonica* on MTL, and autoregressive modeling was applied to all other tree-ring time series to remove autocorrelation from past year’s indices

0.7 for season lengths of 1, 6, 12, and 20 months for *P. arizonica*, and from $r \approx 0.2$ to 0.5 for season lengths of 1, 6, and 12 months for *P. ponderosa* var. *brachyptera*. In contrast, at BIG there were no observed differences between the two species, the significant correlations only occur for season lengths of 1 month and 6 months, and effect sizes were generally lower ($r \approx 0.3$ –0.4; Table 4a, b).

Discussion

Series length, chronology statistics, and growth patterns

The average age of the sampled trees was *c.* 74.5 years. This conservative estimate was obtained from the increment cores, not adjusting for pith. Similar aged cohorts (between sites) were sampled to rule out age-related differences. Sympatric areas (within a site) were sampled to rule out disturbance-related differences, such as insect infestation or fire that could influence the ring-width growth for just one species.

High mean sensitivity and Gini values indicate variability in annual ring widths known as a sensitive growth response to climate. Variability measured as mean sensitivity (MS) is similar to values reported by Fritts (1974) for *P. ponderosa* var. *brachyptera* (average MS = 0.35) and *P. arizonica* (MS = 0.35) populations sampled near our study site at Mt. Bigelow in the early 1960s, which indicate long-term sensitivity to climate and extends the formative work of Fritts. *P. ponderosa* var. *brachyptera* expressed the highest common growth signal based on Rbt (Table 3), which suggests the species is responding to strong external climate signals. The dendroclimatic response varies modestly between species and sites, as quantified by the coefficient of variation, which suggests the two closely related ponderosa pine species have different ecological requirements for growth when sympatric.

Autocorrelation is expected to be higher on extreme sites because stressed trees take a year or more to recover following a harsh growing season, thereby conveying persistent physiological effects (Fritts et al. 1965; Monserud and Marshall 2001). Autocorrelation was significantly higher at Mt. Bigelow than Mt. Lemmon, suggesting the former site is more extreme. Large values of autocorrelation are often explained by the storage of carbohydrates in parenchyma tissue or as the result of temporal autocorrelation found in the precipitation variable (e.g., Matalas 1962; Esper et al. 2015). It is unlikely that annual rainfall is the source of the observed persistence in tree-ring indices because total precipitation between sites is highly correlated. Therefore, the higher value of autocorrelation at Mt. Bigelow is likely caused by biological properties rather than temporal variation in rainfall.

One possible explanation for differences in environmental conditions between sites affecting autocorrelation is the dissimilarity in elevation between the two mountains. The volume of water released after the melt of snowpack is expected to be greater on Mt. Lemmon than Mt. Bigelow as the former is *c.* 250 m higher in elevation with higher snowfall. Also, the AWHC of the soil at Mt. Lemmon (9.2) is

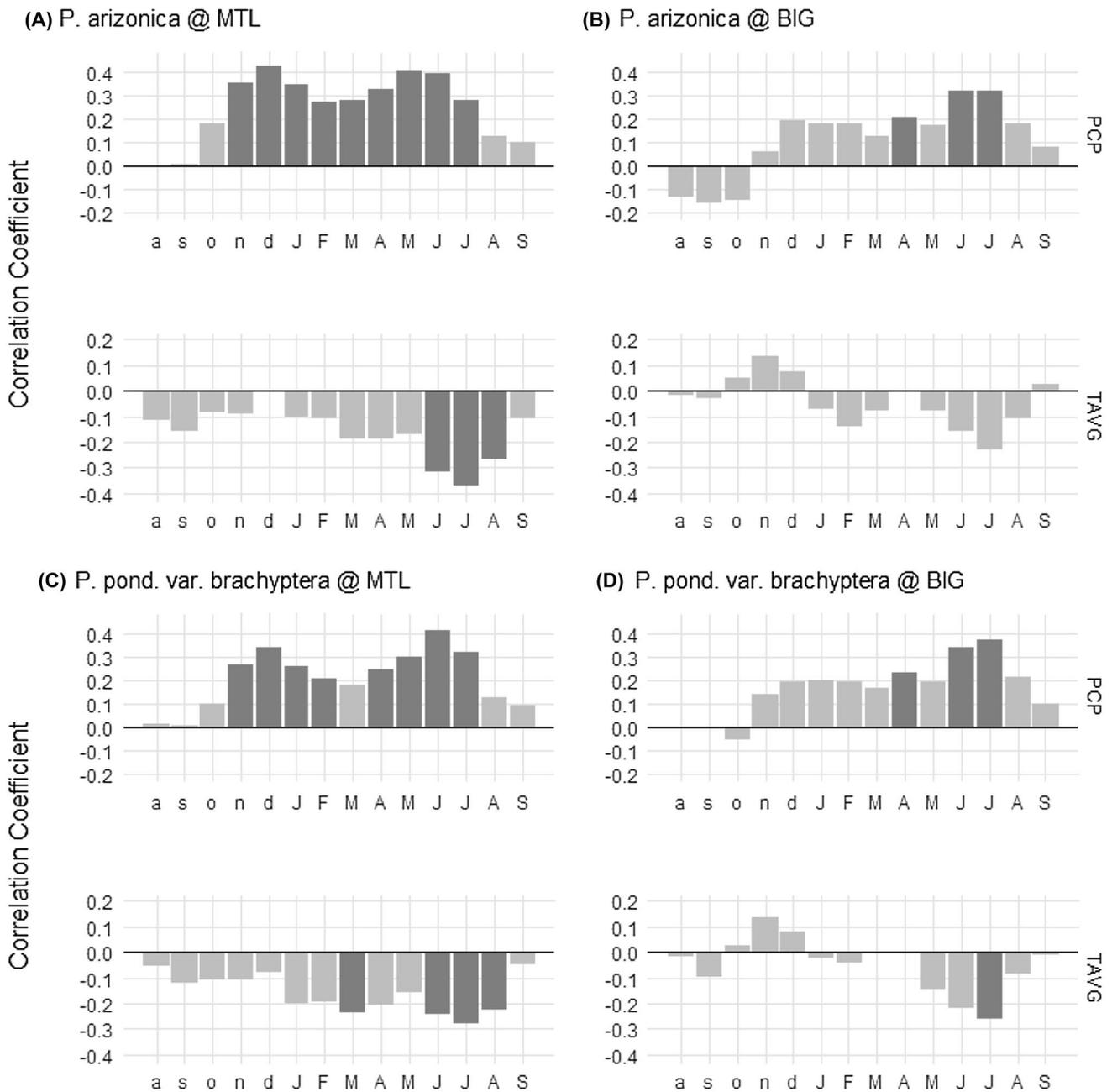


Fig. 4 Climate–growth associations obtained by relating total precipitation (PCP) as primary climate variable (top in each panel) and mean average temperature (T_{AVG}) as secondary climate variable (bottom in each panel) to the ARSTAN ring-width chronologies of *P. arizonica* (a, b) and *P. ponderosa* var. *brachyptera* (c, d) at two sites

MTL (a, c) and BIG (b, d) [Note: Standard chronology for (a)]. PCP was summed and T_{AVG} was averaged for a period of three months whose ending months are shown on the x-axes (previous August–current September). Significant correlations and partial correlations ($p \leq 0.05$) are shown by dark bars

more than two times greater than at Mt. Bigelow (3.8). The combined effect of these features is to increase the storage capacity of the winter snowmelt and prolong the moist conditions of the soil into the growing season when the water demand is highest (Barnett et al. 2005). Thus, the growing environment at Mt. Lemmon may be more favorable for tree species adapted to moister growing conditions.

The two ponderosa pine species experienced recurrent periods of reduced growth. Narrow rings formed during the years 1934, 1936–1939, and 1947–1948 correspond to low annual PDSI values, and past reports of reduced streamflow (1932–1936) and drought (1942–1964) in Arizona (McNab and Karl 1991). In both instances, the drought signals of narrow rings were more pronounced at Mt. Bigelow than Mt.

Table 4 Correlation coefficients of seasonal PDSI with tree-ring chronologies

Site	MTH	LEN	COEF	SIG	LEN	COEF	SIG	LEN	COEF	SIG	LEN	COEF	SIG
(4A) PAZ													
MTL	J	1	0.44	*	6	0.33	*	12	0.29	*	20	0.26	
MTL	F	1	0.45	*	6	0.38	*	12	0.31	*	20	0.29	*
MTL	M	1	0.49	*	6	0.44	*	12	0.34	*	20	0.31	*
MTL	A	1	0.53	*	6	0.48	*	12	0.37	*	20	0.33	*
MTL	M	1	0.59	*	6	0.52	*	12	0.41	*	20	0.36	*
MTL	J	1	0.61	*	6	0.55	*	12	0.45	*	20	0.38	*
MTL	J	1	0.67	*	6	0.58	*	12	0.49	*	20	0.42	*
MTL	A	1	0.58	*	6	0.61	*	12	0.53	*	20	0.44	*
MTL	S	1	0.53	*	6	0.62	*	12	0.56	*	20	0.46	*
BIG	M	1	0.27	*	6	0.21		12	0.15				
BIG	J	1	0.29	*	6	0.23		12	0.17				
BIG	J	1	0.36	*	6	0.26	*	12	0.19				
BIG	A	1	0.31	*	6	0.29	*	12	0.22				
BIG	S	1	0.29	*	6	0.31	*	12	0.24				
(4B) PPB													
MTL	J	1	0.23	*	6	0.06		12	− 0.01		20	− 0.06	
MTL	F	1	0.24	*	6	0.13		12	0.02		20	− 0.03	
MTL	M	1	0.28	*	6	0.20		12	0.05		20	− 0.01	
MTL	A	1	0.33	*	6	0.25	*	12	0.09		20	0.02	
MTL	M	1	0.40	*	6	0.30	*	12	0.14		20	0.05	
MTL	J	1	0.43	*	6	0.33	*	12	0.19		20	0.08	
MTL	J	1	0.48	*	6	0.38	*	12	0.24	*	20	0.12	
MTL	A	1	0.40	*	6	0.40	*	12	0.29	*	20	0.15	
MTL	S	1	0.35	*	6	0.42	*	12	0.32	*	20	0.17	
BIG	M	1	0.31	*	6	0.25		12	0.22				
BIG	J	1	0.32	*	6	0.27		12	0.24				
BIG	J	1	0.39	*	6	0.30	*	12	0.26				
BIG	A	1	0.35	*	6	0.32	*	12	0.28				
BIG	S	1	0.33	*	6	0.34	*	12	0.30				

(A) PAZ *P. arizonica*(B) PPB *P. ponderosa* var. *brachyptera*, MTH month, LEN length of season in months. One-, 6-, and 12-month seasons were analyzed at both sites; 20-month increment is also analyzed at MTL, significance level of 0.05. Partial correlation coefficients for the secondary climate variable (T_{AVG}) are not shown

*Statistically significant

Table 5 Effect sizes (r) of PDSI as a measure of drought sensitivity ($\alpha = 0.05$)

Site	Taxa	Strongest score	Month highest r	r	Strength effect
MTL	<i>P. arizonica</i>	Single month	July	0.67	Large
MTL	<i>P. pond.</i> var. <i>brachyptera</i>	Single month	July	0.45	Medium
BIG	<i>P. arizonica</i>	Single month	July	0.36	Medium
BIG	<i>P. pond.</i> var. <i>brachyptera</i>	Single month	July	0.39	Medium

All p values are highly significant ($p < 0.001$)

Lemmon, a possible result of rockier soils with lower water-holding capacity contributing to lower annual tree-growth at Mt. Bigelow (Candel-Pérez et al. 2012). More recently, growth was reduced during 2002–2009 reflecting severe

drought impacting the entire Southwest region (Woodhouse et al. 2010). Interestingly, the strongest drought signal for the decade is at Mt. Lemmon.

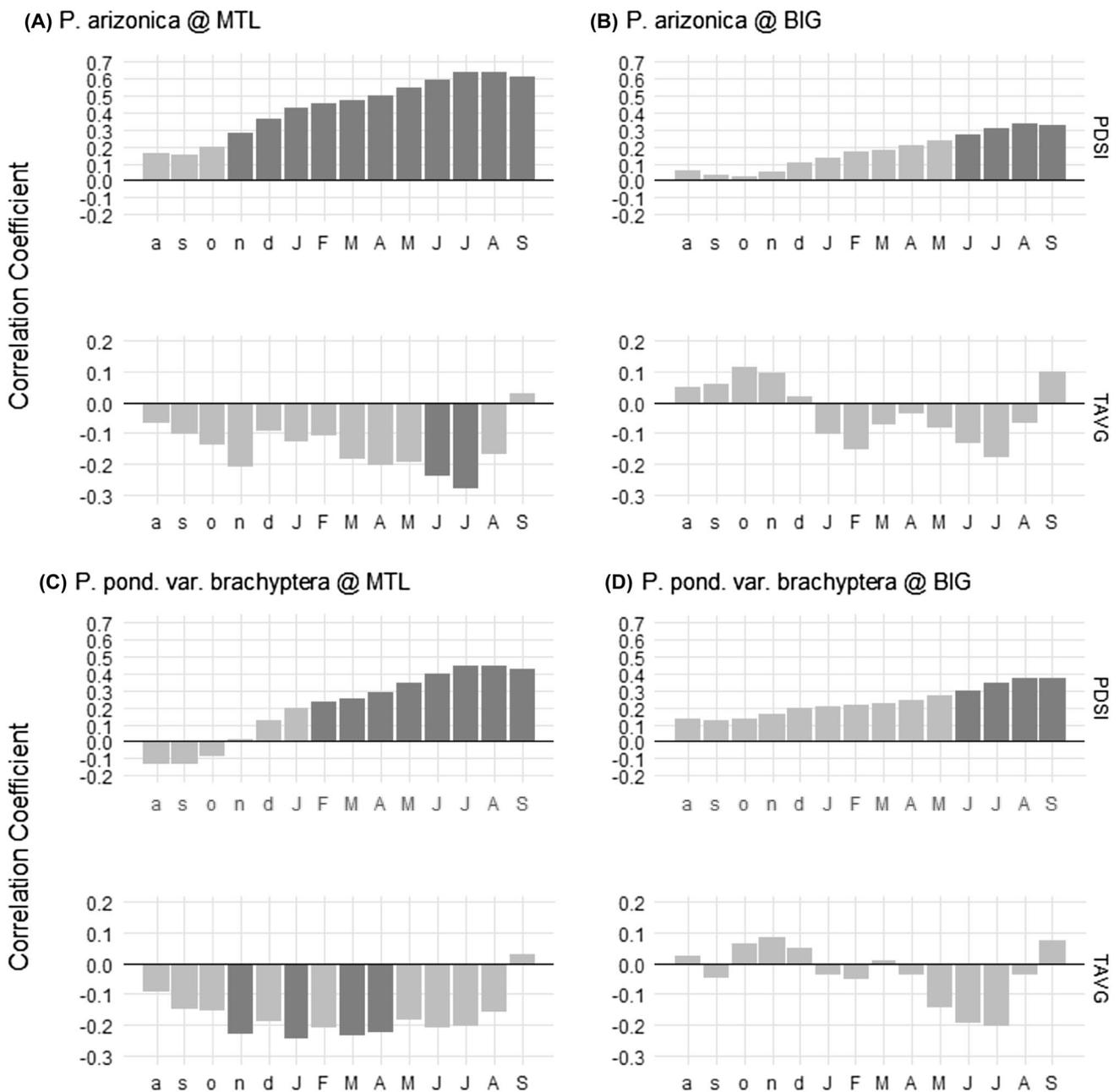


Fig. 5 Climate–growth associations obtained by relating average PDSI as primary climate variable (top in each panel) and mean average temperature (T_{AVG}) as secondary climate variable (bottom in each panel) to the ARSTAN ring-width chronologies of *P. arizonica* (**a, b**) and *P. ponderosa* var. *brachyptera* (**c, d**) at two sites MTL (**a, c**) and

BIG (**b, d**) [note: standard chronology for (**a**)]. PDSI was summed and T_{AVG} was averaged for a period of three month whose ending months are shown on the x-axes (previous August–current September). Significant correlations and partial correlations ($p \leq 0.05$) are shown by dark bars

Fire explains the reversal in site responses observed for the 1930–1940s drought compared to the 2002–2009 drought. The change in growth pattern may have resulted from wildfire decreasing the available soil moisture and amount of photosynthetic foliar tissue, thereby reducing annual growth at Mt. Lemmon. In fact, throughout the early twenty-first century, the Santa Catalina Mountains

were impacted by several large wildfires. These included the Oracle (2002), Bullock (2002), and Aspen (2003) fires. During the peak growing season of 2003, the Aspen wildfire burned the south slope of Mt. Lemmon, including our study site, but left the Mt. Bigelow site relatively undisturbed. The heat of the fire resulted in foliar injury (Telewski, personal observation), which likely decreased cambial growth

through a reduction in foliage and photosynthetic capacity. The formation of a hydrophobic soil layer during wildfire may increase runoff. Dyrness (1976) reported that following a large wildfire in the High Cascades of Oregon, USA (c. 3116 ha), which burned lodgepole pine stands, precipitation runoff increased and recovery (of the soils) was imperceptible until 3–5 years after the fire. The phenomenon of increased runoff would occur even during a drought. Therefore, moisture stress induced by fires in 2003 at Mt. Lemmon would have further reduced observed growth for several more years. Additionally, the PDSI values modeled at Mt. Lemmon would not have captured the effect of increased runoff due to fire because the soil attributes are assumed to be stable.

Response function analysis

Response function analysis indicates strong direct positive correlations between precipitation and annual tree growth, which is consistent with previous reports for ponderosa pine species and moisture limitations in the Southwest (Fritts et al. 1965; Brown 1968; Fritts 1974) and Pacific Northwest (Dannenbergh and Wise 2016). Our study agrees with Brown's (1968) work on ponderosa pine species growing near the summit of Mt. Bigelow, which determined soil moisture is often more limiting to photosynthesis (hence cambial growth) than low air temperatures for semiarid conifers, even in winter. There are seasonal influences and our results show that cool springtime conditions increased the inter-annual growth for both taxa (April–June) and demonstrate seasonal variation for the lower elevation species (*P. arizonica*). *P. arizonica* is also sensitive to winter moisture at Mt. Lemmon, which implies growing season use of winter water extracted from deep soil for growth (previous November–March). Response function analysis indicates early-winter precipitation (previous October–previous December) was influencing the growth of *P. arizonica* as opposed to late winter (January–March), which suggests that snow melt was not a major factor in the species response to winter climate. Although responses to temperature were weaker than to precipitation, Fig. 3 shows a growth reduction occurred for *P. arizonica* when minimum spring temperature (April–June) rose above a critical level at Mt. Lemmon. The observed reduction in correlations between tree rings and minimum temperature has been reported in other southwestern ponderosa pine studies and is explained by increased respiration or drought stress (Fritts 1974, 1976; Adams and Kolb 2005), which negatively affected the growth of *P. arizonica* but not *P. ponderosa* var. *brachyptera*.

Correlations to climate

Analysis of seasonal response functions of ponderosa pine indicated that high precipitation during the cool-moist

conditions of winter (November–March), and spring (April–June) are most important for tree growth. Our results broadly agree with González-Cásares et al. (2017) who reported maximum positive correlation for the 9-month period ending in June (October–June) for the annual growth of *P. arizonica* in northwestern Mexico.

Further analysis of the climate–growth relationships with correlation analyses indicated that the annual growth of the ponderosa pine species was under significant moisture stress in spring. The strong positive correlation to spring precipitation and negative partial correlation to spring temperature indicates that the semiarid local climate of the Santa Catalina Mountains has negatively impacted the growth of *P. ponderosa* var. *brachyptera* growing at its lower elevational limit. In comparison, the growth of *P. arizonica* growing at its upper elevational limit was only impacted at Mt. Lemmon. A consistent temperature signal is lacking for the tree-ring indices at Mt. Bigelow, demonstrating differences in habitat suitability between sites for ponderosa pine growth.

These results correspond to the conceptual models of Fritts (1974, 1976) that describe the relationships leading to moisture stress prior to or during the growing season, resulting in the formation of narrow rings. High temperature and low precipitation are primarily responsible for decreased growth of semiarid site conifers. With these models in mind, we considered drought conditions in spring, which can lead to high evapotranspirational demand and the formation of narrow rings during the growing season.

Sensitivity to PDSI

Pinus arizonica and *P. ponderosa* var. *brachyptera* are drought-sensitive species (Peltier et al. 2016), which show strong positive PDSI-growth correlations, although the climate–growth relationships vary between species at Mt. Lemmon. The PDSI-growth correlations did not support our hypothesis that *P. ponderosa* var. *brachyptera* would be more sensitive to soil moisture availability. *P. arizonica* has a stronger long-term relationship, while *P. ponderosa* var. *brachyptera*'s correlations were for a shorter duration and weaker. There are differences between sites; correlation to drought lasts longer at Mt. Lemmon than Mt. Bigelow, regardless of species.

A multi-species synthesis of ring-width variance has shown that *P. ponderosa* has low resistance and slow recovery to drought (Peltier et al. 2016). Similarly, the observed extended correlation of growth with PDSI in this study implies that *P. arizonica* and *P. ponderosa* var. *brachyptera* may be vulnerable to changing climate (González-Cásares et al. 2017). Thus, warmer conditions may have a more negative effect on *P. arizonica*, as periods with low PDSI become longer or more common. Other studies have noted differences in growth sensitivity to climate for the *Pinus* species

of Mexican pine forests (Bickford et al. 2011; González-Cásares et al. 2017). These dissimilarities have been partially credited to different drought tolerances of the species under study. Although more work is required to build the appropriate models, the length of correlation to PDSI could be one factor useful in determining tolerance to moisture stress.

It is interesting that tree growth correlated to PDSI for the longest period at Mt. Lemmon, the more favorable site. Although not as extreme as the crevice sites in the Western USA described by Fritts (1976), the ponderosa pine species of Mt. Bigelow also grow in an extreme environment with shallow, rocky soils, and restricted root space. Though counterintuitive, Fritts' (1976) description of crevice sites in Arizona describes dry soils as constraining root and crown growth for longer periods of time, and trees acclimate to these conditions so that growth responses to precipitation will be less vigorous than trees growing on more favorable sites. Thus, trees growing on more favorable sites will suffer more stress from drought than trees growing on drier sites, which have acclimated to low water availability. Therefore, one reason for the longer drought influence at Mt. Lemmon is the greater loss of green needle tissue related to prolonged water stress. This hypothesis of reduction in photosynthetic capacity is supported by Galiano et al. (2011) who determined that carbon reserves are key to tree recovery and forest resilience following periods of drought; consequently, respiration will influence carbon reserves and tolerance to moisture stress.

Respiration

Temperatures on south-facing slopes may exceed the optimum range for plant processes during the growing season or winter months (Fritts 1974). Therefore, slope aspect greatly affects the correlation of ring widths with climate, and annual ring widths are expected to correlate negatively with variations in monthly temperature. The conceptual models of Fritts (1974, 1976) describe the pathways leading to increased respiration, and the formation of narrow rings. These negative temperature effects on growth are apparent during the growing season due to high temperature and respiration reducing the plant photosynthetic processes (Fig. 1 of Fritts 1974). Negative growth effects are also expected from elevated temperatures during the winter months (i.e., prior to the growing season) due to the direct effects of warm air temperature on respiration resulting in increased carbon consumption and decreased carbon allocation; consequently, cold hardiness is reduced (Fig. 2 of Fritts 1974; Ögren et al. 1997). Our results support Fritts' model of growing season respiration and winter respiration. The correlation analysis indicated

growth of *P. arizonica* was limited by spring and summer drought stress (+, PDSI) and temperature (–, T_{AVG}) at Mt. Lemmon, an indication of increased respiration during the growing season. In comparison, *P. ponderosa* var. *brachyptera* was limited by moisture stress (+, PDSI) and temperature (–, T_{AVG}) during Mt. Lemmon's winter season. Thus, the two species are responding differently to water balance requirements and carbon limitations. The most common cause of increased evapotranspirational demands is high air temperature at low elevations, which may cause increased moisture stress in spring and summer (*P. arizonica*) and decreased cold tolerance in winter (*P. ponderosa* var. *brachyptera*).

Conclusions

The growth of the two species responded positively to the cool-wet conditions of spring, and winter precipitation also improved the growing conditions for *P. arizonica*. We did not find support for higher climate sensitivity in *P. ponderosa* var. *brachyptera* (at its lower elevational limit) above that observed in *P. arizonica* (at its upper elevational limit). However, we report small differences in ring-width variances between *P. ponderosa* var. *brachyptera* and *P. arizonica*, and that both species are sensitive to the negative effects of respiration on annual growth in different seasons, winter and summer, respectively. Notably, rising night-time temperatures during springtime reduced growth for *P. arizonica* but not *P. ponderosa* var. *brachyptera* at Mt. Lemmon, most likely from increased respiration or moisture stress. Tree rings correlated to PDSI at different temporal scales, which suggests that *P. arizonica* is sensitive to drought for longer periods. Although our data did not support our hypothesis that *P. ponderosa* var. *brachyptera* would be more sensitive to soil moisture availability, the temporal differences in drought sensitivities distinguish the two taxa by their varying tolerances to water shortages. Both species exhibit a stronger climatic response at Mt. Lemmon (the less dry site) than Mt. Bigelow, and moisture availability between sites can be further influenced by disturbance. In summary, the growth of *P. ponderosa* var. *brachyptera* and *P. arizonica* at their transition zone demonstrated subtle, biologically meaningful differences in seasonal precipitation requirements for growth, sensitivity to moisture stress and tolerance to cold temperatures.

Author contribution statement PM conceived the study; PM and FT designed the experiments and collected samples in the field; PM led and SJ and GT assisted with preparing the samples; PM led and BM assisted with data analysis; PM wrote the paper; and BM, FT, SJ, and GT edited the paper.

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Data availability The tree-ring datasets generated and analyzed during the current study are available from the International Tree-Ring Data Bank (ITRDB) repository, <https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>. These datasets include the raw ring widths for 90 trees (204 radii) and 4 composite chronologies listed in “Methods” (see Tree Growth Data).

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

Appendix 1: Validation of climatic data

Soils data used in the West Wide Drought Tracker PDSI calculation were obtained from Penn State University (Abatzoglou et al. 2017). The applicability of the 4-km resolution PDSI data was assessed by comparing the AWHC values of the specific soil units in the calculation (Abatzoglou et al. 2017) to those represented in the local soils plots near the research sites ($n = 180$; 60 trees \times 3 sites; Top panel; Suppl. Figure 1). The soils data used in the PDSI calculation indicate AWHC of 6.0% for the area encompassing the study sites. The modeled PDSI data were validated by interpolating AWHC values from soil pedons sampled from the Coronado National Forest ($n = 14$; Lower Panel; Suppl. Figure 1) and averaging the interpolated values for sampled tree locations ($n = 120$; 60 trees \times 2 sites; AWHC = 5.9%). Precipitation and T_{AVG} data were validated by correlating the modelled site data with locally collected weather data that were accurate but too short for tree-ring analysis. Palisades’ 17 years of PCP data (1965 to 1981) collected at 2425 m a.s.l. within 0.7 km of the study sites (Vose et al. 2014), were used to validate the monsoonal patterns (Suppl. Figure 2A). Kitt Peak’s 56 years of climate data (1960 to 2015; Vose et al. 2014) within c. 95 km and similar in elevation (2070 m) to the study sites, were used to validate winter PCP and T_{AVG} (Suppl. Figure 2B, 2C). Pearson correlations were applied to validate the gridded climate dataset (McKenney et al. 2011). Correlations were consistently highest for the McKenney/NOAA PAL associations. Same month–month correlations are positive and range from 0.8 (June–June) for the T_{AVG} association (Suppl. Figure 2C),

to 1.0 (e.g., Feb.–Feb.) for the PCP associations (Suppl. Figure 2A). The strength of the collinear correlation is weakest for June–June PCP for the McKenney Mt. Lemmon/Kitt Peak dataset (0.52; Suppl. Figure 2B) because summer monsoon strongly influences Mt. Lemmon’s climate but not Kitt Peak’s.

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