



Variable growth responses of four tree species to climate and drought in a Madrean pine-oak forest

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ABSTRACT

The tolerance of tree growth to drought in diverse mixed forests subjected to seasonal water shortage is understudied despite their ecological and economic relevance. By combining intra- and inter-annual analyses of radial growth responses to climate and drought at daily and monthly scales, different strategies to acclimate to hydroclimate variability of coexisting conifers and broadleaves were unveiled. We analyzed the growth patterns and responses to hydroclimate variability in two conifers (*Pinus engelmannii*, *Juniperus deppeana*) and two broadleaves (*Quercus grisea*, *Arbutus arizonica*) co-occurring in a Madrean pine-oak forest located in NW México. The strongest positive response to daily precipitation was found in the two conifers, but this response peaked earlier in *J. deppeana* than in *P. engelmannii*, which presented a more delayed formation of radially-enlarging tracheids. The latest negative response to temperature was found in *Q. grisea*, which agrees with its more delayed xylogenesis than *A. arizonica*. *P. engelmannii* presented the highest responsiveness to water shortage, driven by lower precipitation and high maximum temperatures, responding to longer droughts ending in autumn ($r = 0.72$), whilst *A. arizonica* showed the lowest responsiveness to short spring droughts ($r = 0.39$). Growth of *P. engelmannii* was linked to climate-atmospheric circulation patterns over the near Pacific Ocean. Overall, *P. engelmannii* and *A. arizonica* showed high growth rates and earlier growth onset, whilst *J. deppeana* and *Q. grisea* showed slower growth rates and later growth onset. The Vaganov-Shashkin growth model evidenced that winter-spring soil moisture was the key driver of growth. Under more arid conditions and more frequent and hotter droughts, pine stands could rapidly shift towards mixed pine-oak forests.

1. Introduction

Increasingly warmer and drier conditions are amplifying the severity and duration of droughts through increased evapotranspiration rates affecting megadiverse countries such as México (Seager et al., 2009; Dobler-Morales and Bocco, 2021). In this country, many extratropical mixed forests are dominated by conifer and hardwood tree species which are vulnerable to drought stress inducing a reduction in radial growth and a loss of resilience (Acosta-Hernández et al., 2019, 2024; Correa-Díaz et al., 2023; Pompa-García et al., 2021, 2023a, 2023b). Mexican pine-oak forests constitute paradigmatic examples of vulnerable ecosystems with numerous ecological and economic values for local communities (Galicia et al., 2015; Martin et al., 2021). It is known that coexisting conifer and

hardwood species are adapted to tolerate seasonal water shortages using different mechanisms. For instance, oaks uptake water from deeper sources than pines during dry periods (Del Castillo et al., 2016). In central México, oak species from arid areas show higher leaf deciduousness and water-use efficiency and form a xylem more resistant to embolism than their humid counterparts (Aguilar-Romero et al., 2017). In oaks, niche partitioning among phylogenetically similar species has been linked to trade-offs between drought avoidance or tolerance (desiccation recovery) and growth rates (Fallon and Cavender-Bares, 2018). Ring-porous oaks are typically considered anisohydric species, i.e. their leaf water potential decreases during drought (as soil water potential declines), but the stomatal conductance is kept relatively high sacrificing xylem safety (increased risk of xylem cavitation), whereas pines are isohydric species

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limiting gas exchange during drought (Quero et al., 2011; Klein, 2014; Roman et al., 2015). Other less studied sympatric species also show contrasting water-use strategies in response to drought such as junipers and diffuse-porous broadleaves (e.g., *Arbutus* species) which tend to follow anisohydric and isohydric strategies, respectively (Raimondo et al., 2015; Voelker et al., 2018). In summary, the different anatomical, phenological and ecophysiological mechanisms to tolerate drought stress must be considered when assessing xylogenesis of coexisting tree species in order to forecast their growth responses to expected aridification trends.

Mixed conifer-hardwood forests are still understudied regarding their intra- and inter-annual radial growth patterns and responses to climate variability, particularly seasonal water shortage and atmospheric drought (vapor pressure deficit, VPD). Quantifying how intra- and inter-annual growth responses to climate and water limitation vary among coexisting tree species can contribute to understanding how diversity is maintained through temporal sharing of niches and to forecast how this coexistence could change under drier conditions (Schwinning and Kelly, 2013). Here, we determine if differences in growth sensitivity to drought affect temporal resource heterogeneity of two conifers (*Pinus engelmannii*, *Juniperus deppeana*) and two hardwood species (*Quercus grisea*, *Arbutus arizonica*) coexisting in a Madrean pine-oak forest. Specifically, we aim: (1) to analyze xylogenesis in the four species, (2) to relate series of growth indices with climate variables at daily and monthly resolutions, and (3) to fit a growth model to pinpoint the main climate drivers of growth during the growing season. The second objective is complemented with analyses between growth and teleconnection indices to frame our analyses in a regional context given the relevance of the Monsoon summer rainfall for the study forests (Seager et al., 2009; Szejner et al., 2020; Pompa-García et al., 2021). Furthermore, hydroclimate variability in the region can be linked to atmospheric teleconnections driven by sea surface temperature (SST) variability across the Pacific Ocean (Castro et al., 2001). To fulfill the third objective, we use the Vaganov-Shashkin model (hereafter VS model), which is a process-based model explicitly considering nonlinear relationships between climate and radial growth (Vaganov et al., 2006; Tychkov et al., 2019). We expect different growth responses to climate of coexisting tree species at intra- and inter-annual scales. Specifically, we hypothesize that species showing an earlier growth onset would be those showing higher growth rates and be more responsive to winter-spring drought, whereas late-growing species would be less responsive.

2. Material and methods

2.1. Study area

We selected a mixed conifer-hardwood forest located in the Sierra Madre Occidental, NW México (Mesa de Pawiránachi, 107.116° W, 27.130° N, 2,400 m a.s.l.). The site is located in the municipality of Guachochi (Chihuahua State), and it is owned by the local community which provided the sampling permission. The selected study site is homogeneous in terms of local climatic conditions, vegetation composition and soil type. This forest is located on a volcanic plateau and it is dominated by several coexisting pine and oak species with accompanying juniper and *Arbutus* species characterizing typical Madrean pine-oak forests (González-Elizondo et al., 2012).

Here, we sampled two evergreen conifers (*Pinus engelmannii* Carrière., *Juniperus deppeana* Steud.) and two broadleaves (the deciduous or sub-evergreen *Quercus grisea* Liebm. and the evergreen *Arbutus arizonica* (A. Grey) Sarg.). The study pine (*P. engelmannii*) and juniper (*J. deppeana*) are distributed from the SW U.S.A. to SW México, mainly in mesic sites at an elevation range of 1,200–3,000 m a.s.l., in locations with deep and well-drained soils, often forming post-fire mixed stands (Barton, 2002; García and González, 2003). The study oak (*Q. grisea*) is found in moist sites of canyons and mountain areas (1,500–2,500 m a.s.l.) from SW U.S.A. to central México. It grows as a tree or shrub and shows considerable

tolerance to prolonged summer drought stress (Fallon and Cavender-Bares, 2018). The madrone (*A. arizonica*) is a short, evergreen tree or shrub found in a similar geographic area as the oak and abundant in canyon bottoms and hillsides (1,200–2,500 m a.s.l.). *Q. grisea* and *A. arizonica* form ring-porous and diffuse-porous wood, respectively (Pompa-García et al., 2023a).

The study region has a temperate, sub-humid climate with cool and wet summers due to the influence of the North American Monsoon from June to September, whereas winters (November to February) are cold and dry (Seager et al., 2009). The study site presents a mean annual temperature of 13.6 °C, and total annual precipitation of ca. 1,100 mm (Fig. S1). Summer and winter account for 35% and 14% of the total annual precipitation, respectively. The soils correspond to the luvisol type, with high clay content (González-Cázares et al., 2020). The study area has great ecological, economic and environmental values, given the diversity of conifer and hardwood tree species and the ecosystem services of these mountain forests including remarkable timber yields (SEM-ARNAT, 2016). The study site is neither managed nor used for timber production.

2.2. Field sampling

Sampled trees were dominant and apparently healthy and did not present any indication of drought-induced dieback. From late autumn to winter 2019, 14 to 22 trees per species were sampled at breast height (1.3 m) using a 5-mm Pressler increment borer. Two cores per tree were taken. The sampling stands encompassed a ca. 3 ha large area.

2.3. Xylogenesis

We selected five dominant mature trees per species, not sampled for tree-ring measurements but of similar size and social status, to carry out the xylogenesis assessment. Therefore, a total of 20 trees (5 trees per species) were sampled. Sampling started on August 25, 2022 and ended on October 15, 2023. It was done at biweekly resolution leading to 26 sampling campaigns. During the sampling period, climate conditions were slightly warm in winter 2022–2023 and warm and dry in summer 2023 (Fig. S2).

To assess xylogenesis, microcores with a diameter of 2 mm and a length of 15 mm containing the intact cambium and several rings were collected at 1.0–1.3 m using a Trephor® corer (Rossi et al., 2006; Deslauriers et al., 2015). Wood samples were taken along a spiral with a distance of 5–10 cm among consecutive sampling positions to avoid the impact of local wound reactions on intra-annual growth dynamics.

Microcores were placed into Eppendorf tubes with 50% ethanol solution and stored at 5 °C. They were dehydrated in successive ethanol solutions (70%, 85%, 95% and 100%). Transverse sections with a thickness of 10–15 µm were cut using a rotary microtome (RM2245, Leica, Germany), stained with safranin red and astra blue, and mounted on glass slides using Eukitt® mounting medium (Sigma, Germany). The wood sections were analyzed under normal and polarized light using a microscope equipped with a digital camera (DM2500, Leica, Germany). Cambial cells and radially enlarging cells were stained in blue, cell-wall thickening cells were stained partly blue and partly red, and mature lignified tracheids were stained in red. We counted and averaged the number of cells located in the cambial zone, the radially-enlarging zone, and the cell-wall thickening zone along five radial rows per sample, as well as the thickness of the current and previous annual rings. This was done using the ImageJ software (Schneider et al., 2012).

In the two conifers and along five radial lines per ring, the number of cambium cells, radially enlarging tracheids, wall-thickening tracheids, and mature cells were counted and an average was made (Camarero et al., 2010). Mature earlywood (EW) and latewood (LW) tracheids were distinguished according to their lumen and cell wall thickness (Denne, 1989). During xylem development, cells show different shapes and stain with different colors (Antonova and Stasova, 1993): cambial cells are

bone-shaped and present small radial diameters and thin walls; radially elongating tracheids show wide diameters and thin primary walls; wall-thickening tracheids are characterized by cell wall corner rounding; secondary walls glisten under polarized light and walls turn blue due to lignification; lastly, mature cells show completely blue walls.

In the two broadleaves, the number of cambial cells was counted and the EW and LW widths were measured under the microscope following Frankenstein et al. (2005) and Pompa-García et al. (2023a). The key dates of xylogenesis phases are given as calendar or Julian days (DOY, day of the year).

2.4. Climate data, drought and teleconnection indices

We obtained daily and monthly climate data (mean temperature; TMx, mean maximum temperature; TMn, mean minimum temperature; Pre, total precipitation) from the nearby “El Salto” station (23°47' N, 105°22' W, 2,560 m a.s.l., period 1979–2019). To fit the VS model, long-term, homogeneous daily data (mean temperature, precipitation) were obtained from the 30-km-gridded ERA5 climate dataset (Hersbach et al., 2020).

To assess drought severity and duration we used monthly, 0.5°-gridded data of the Standardized Precipitation Evapotranspiration Index (SPEI). The SPEI is a multi-scalar drought index computed from monthly rainfall, temperature, and potential evapotranspiration showing cumulative water surplus or deficit (Vicente-Serrano et al., 2010).

To determine how climate-atmospheric circulation patterns drive climate variability and tree growth we obtained several indices following previous studies (González-Casares et al., 2017): the Southern Oscillation Index (SOI), which is based on the sea level pressure and temperature differences between the western and eastern tropical Pacific (Ropelewski and Jones, 1987); the El Niño 3.4 index based on the SST anomalies in the “El Niño 3.4” region (5° N – 5° S, 120°–170° W) situated across the equatorial Pacific (Rayner et al., 2003); and the Pacific Decadal Oscillation (PDO) which is a long-term El Niño-like pattern of climate variability characterized by warm and cool SST anomalies in the tropical Pacific Ocean (Zhang et al., 1997). Spatial field correlations were also calculated between chronologies and SSTs obtained from the 0.25°-gridded NCEP-NOAA dataset for the period 1981–2019 (Reynolds et al., 2007).

2.5. Tree-ring methods

To process wood samples and obtain precisely dated annual tree-ring width data we used dendrochronology (Fritts, 1976). The wood samples (cores) were air dried and mounted on wooden grooves. The cores were polished with sandpapers of progressively higher grain (60–1,000 grit) to highlight their growth rings. The rings were visually cross-dated (Stokes and Smiley, 1968) and their widths were measured with a resolution of 0.01 mm using a Velmex system. The dating was checked using the program COFECHA, which compared the series of each tree to a master chronology of each species (Holmes, 1983).

The most difficult cross-dating corresponded to the juniper, which often showed eccentric growth, and the madrone because it did not always form conspicuous ring boundaries. In the case of the pine, we detected several intra-annual wood density fluctuations or false rings. In all cases, we were able to produce robust and coherent species' chronologies.

To assess growth trends, we converted the individual ring-width series into mean basal area increment (BAI) series for each site and species assuming a concentric stem growth. In cores without pith, we corrected the BAI by estimating the length of the missing radius using a graphical method, already tested on oak species, which is based on the convergence of rays towards the pith (Rozas, 2003). Tree age was estimated based on the oldest, cross-dated core per tree after correcting the missing innermost rings using this graphical method.

To calculate climate- and drought-growth relationships each tree-ring

width series was detrended by fitting 30-year cubic smoothing splines with a 50% frequency response cut-off. Ring-width indices were obtained by dividing observed by fitted values. Growth persistence in the series of indices was removed by autoregressive modeling, and the resulting pre-whitened or residual series of ring-width indices were averaged using a biweight robust mean to obtain residual series (chronologies) for the four study species. The quality of the chronologies was assessed by calculating several statistics (Fritts, 1976; Cook and Kairiukstis, 1990): first-order autocorrelation of raw data (AC1), mean sensitivity (MS) of ring-width indices without removing temporal autocorrelation, and mean correlation between series (rbar). In all species, the chronologies showed an Expressed Population Signal over 0.85 for the common period 1980–2019, indicating they are well replicated and share a common signal (Wigley et al., 1984). These procedures were developed with the dplR library (Bunn, 2008, 2010; Bunn et al., 2024) of the software R (R Development Core Team, 2024).

2.6. Climate- and drought-growth relationships

To assess climate-growth relationships at the inter-annual scale, Pearson correlations were calculated. Climate-growth correlations were based on daily or monthly temperature and precipitation data considering the common period 1980–2019. In the case of daily data, we used the dentroTools R package to obtain the optimal time window corresponding to the dates when the highest Pearson correlation coefficient was obtained (Jevšenak and Levanič, 2018; Jevšenak, 2020). The selected climate window for analyses considering monthly climate variables included from the previous August to the current September. To emphasize year-to-year climate variability, monthly climate variables were detrended using linear regressions. The resulting climate residuals (differences between observed and fitted values) were used to calculate climate-growth relationships using the treeclim R package (Zang and Biondi, 2015).

We also calculated drought-growth relationships at monthly scales based on Pearson correlations and using again the treeclim R package. In this case, we considered the climate window from January to December and used SPEI values calculated at 1- to 24-month long scales.

2.7. Using the Vaganov-Shashkin model to pinpoint the climate drivers of growth

We used the VS model to estimate intra-annual growth rates and to infer their main climate drivers. This model has been successfully used in conifers (e.g., Valeriano et al., 2023a) and broadleaves (e.g., Tumajer et al., 2022), albeit it was originally conceived for conifers (Vaganov et al., 2006). The chronology of each species was used to fit the VS model as a function of daily temperature and precipitation. The parameterization of the model was done with the software VS-Oscilloscope ver. 1.37 (Shishov et al., 2016), which allows maximizing the correlation between observed and simulated chronologies. The daily growth rate (Gr) was estimated as a function of three partial growth rates that depend on daily temperature (GrT), soil water content (GrW), and photoperiod which did not change over the years and it is calculated as a function of site latitude. Lower GrT or GrW values indicate growth is more constrained by low temperatures or low soil moisture, respectively. The best-replicated common period (1980–2019) was used for fitting the VS model. Two 20-year long sub-periods were considered for calibration (1980–1999) and verification (2000–2019). A simple optimization algorithm was applied for tuning 17 parameters, whereas the rest of the parameters were kept constant (Table S1). To ensure that all models were tuned under similar conditions, the initial parameter values, the random seed (999), and the number of iterations (999) were the same for all models. In addition, only a single parameter was adjusted at a time, while the remaining parameters assumed the previously optimized values. Finally, to evaluate model fitness by comparing observed and simulated series of ring-width indices, three statistics were calculated considering the whole

period (1980–2019) and also calibration (1980–1999) and verification (2000–2019) periods: Pearson correlation coefficient (r), root-mean-square error (RMSE), and Gleichläufigkeit (Glk). The RMSE is a quadratic scoring rule measuring the average magnitude of error between observed and predicted values. The Glk is a synchronicity index which measures the percentage of common signs of year-to-year growth change between two series (Buras and Wilmking, 2015).

2.8. Statistical analyses

To explore the relationships between species' chronologies and to highlight years of high growth rates a Principal Component Analysis (PCA) was conducted on the variance-covariance matrix of the species' residual chronologies (period 1980–2019). Then, the scores of the first (PC1) and second (PC2) principal components of the four species and the annual ring-width indices were plotted in a biplot to examine their relationships. The PCA was performed using the vegan R package (Oksanen et al., 2024).

A Superposed Epoch Analysis (SEA) was applied to calculate growth departures for drought years as compared with climatically normal years. We considered several drought years (1980, 1982, 1989, 1996, 1999, 2000, 2002, 2011, and 2017), defined as those with 14-month October SPEI ≤ -0.5 (Fig. S3). Five of the nine drought years were within 1–2 years of each other (e.g., 1980 and 1982, 1999–2000–2002), which means that “pre-drought” or “post-drought” periods of a given drought may include another drought. To assess their impacts, the SEA was repeated using non-overlapping drought years (1980, 1989, 1999, 2011 and 2017). In the SEA, the response is shown as a deviation of climate conditions prior to and following event years (e.g., droughts, fires) (Lough and Fritts, 1987). The SEA output corresponded to actual minus simulated departures of ring-width indices for the three previous and subsequent years considering the four species and the common period 1980–2019. To determine if ring-width indices for dry years significantly

differed from randomly selected sets of lag ± 3 years, bootstrap resampling (1000 Monte Carlo simulations) was used to estimate the significance for the departures from the mean ring-width index. The SEA was conducted using the dplR package.

3. Results

3.1. Xylogenesis

Radially-enlarging tracheids were observed from April to June in *J. deppeana* and *P. engelmannii*, respectively, with cambium cells and enlarging tracheids peaking from May to September (Figs. 1 and 2). In these two conifers, cell-wall thickening tracheids were formed from July to November and peaked in August. The maximum rates of production of mature EW and LW tracheids were observed in August–September and October, respectively. In the two broadleaf species, cambium cells peaked in April (*A. arizonica*) or June (*Q. grisea*), the EW started to form in April and its rate of formation peaked in May (Figs. 1 and 3). In the case of LW, it started forming in early June and its rate of formation peaked in mid-July.

3.2. Growth patterns

The highest growth rates corresponded to *P. engelmannii*, which also showed the widest stems, followed by *A. arizonica* (Table 1). Overall, sampled trees were relatively young with a mean age of 42–60 years. No significant difference was found between species regarding AC1 (Kruskal-Wallis test, $\chi^2 = 3.8$, $p = 0.284$), whereas the MS peaked in *J. deppeana*. The highest rbar values corresponded to *P. engelmannii*.

Regarding BAI trends, only *Q. grisea* showed a significant linear positive slope (0.067, $p = 0.0001$). The species' chronologies showed a high coherence with positive and significant correlations found between most pairs of species except *P. engelmannii* and *J. deppeana* ($r = 0.25$, $p =$

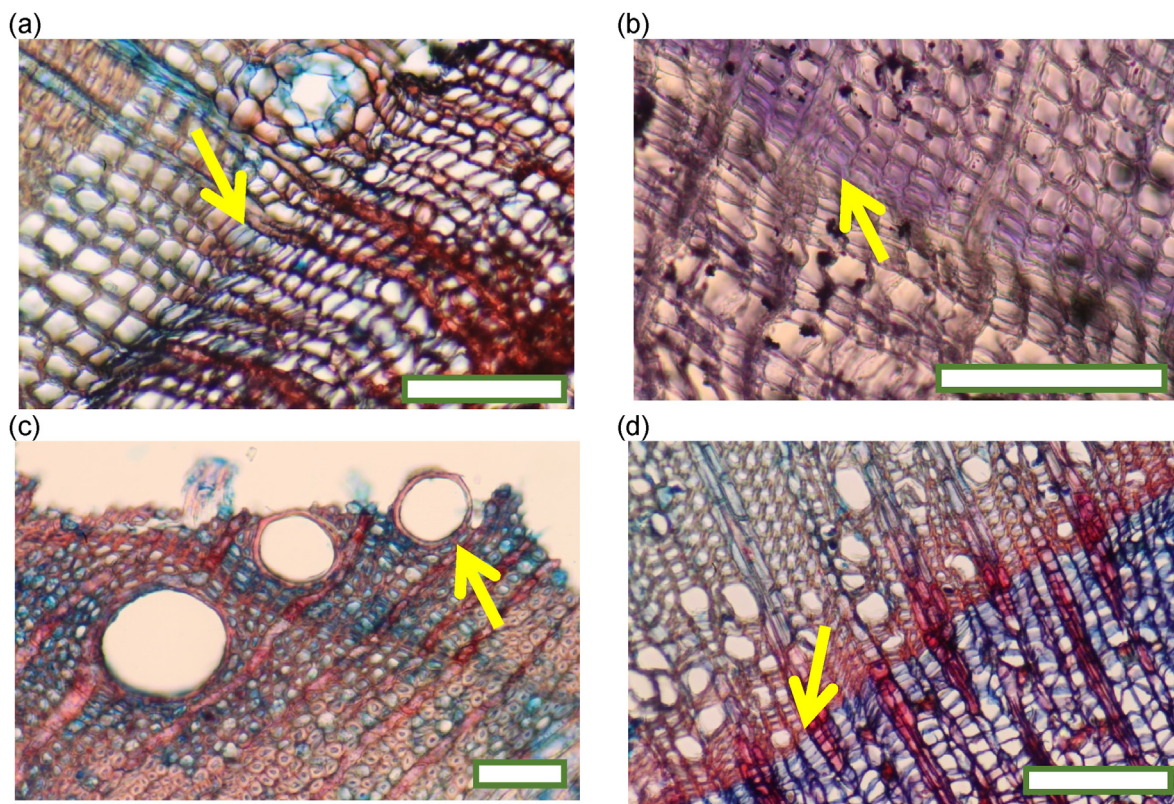


Fig. 1. Cross-sections of the study species showing recently formed xylem cells (yellow arrows) in: (a) *Pinus engelmannii* (early June), (b) *Juniperus deppeana* (mid-April), (c) *Quercus grisea* (mid-May) and (d) *Arbutus arizonica* (early May). White bars represent 50 μm .

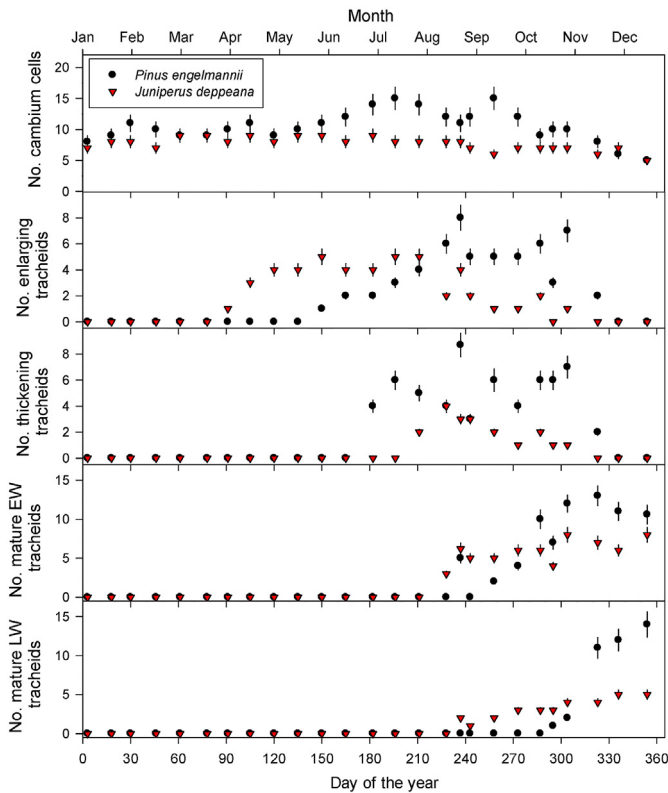


Fig. 2. Xilogenesis patterns in the two study conifers. EW and LW are earlywood and latewood, respectively. Values are means $\pm$ SE.

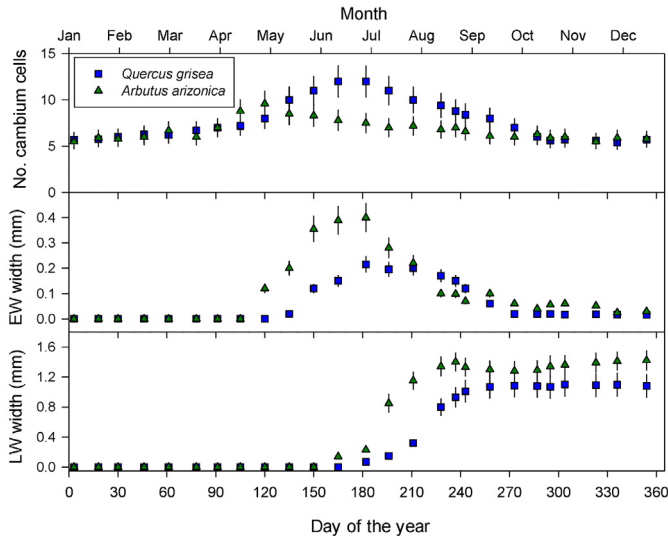


Fig. 3. Xilogenesis patterns in the two study broadleaf species. EW and LW are earlywood and latewood, respectively. Values are means $\pm$ SE.

Table 1
Values are means $\pm$ SD. BAI is the basal area increment calculated for the common period (1980–2019), AC1 is the first-order autocorrelation, MS is the mean sensitivity, rbar is the mean correlation between series. Different letters indicate significant ($p < 0.05$) differences between species according to Mann-Whitney tests.

Species	Dbh (cm)	No. trees (No. radii)	Timespan	Age (years)	Tree-ring width (mm)	BAI (cm ² ·yr ⁻¹)	AC1	MS	rbar
<i>Pinus engelmannii</i>	36.2 $\pm$ 4.5b	22 (42)	1930–2019	60 $\pm$ 13b	2.13 $\pm$ 0.52b	17.31 $\pm$ 7.24b	0.39 $\pm$ 0.20a	0.46 $\pm$ 0.08a	0.68
<i>Juniperus deppeana</i>	17.0 $\pm$ 3.9a	15 (29)	1937–2023	45 $\pm$ 16 ab	1.40 $\pm$ 0.50a	8.08 $\pm$ 4.34 ab	0.41 $\pm$ 0.18a	0.61 $\pm$ 0.09 ab	0.44
<i>Quercus grisea</i>	13.5 $\pm$ 2.0a	14 (28)	1975–2022	42 $\pm$ 3a	1.21 $\pm$ 0.32a	2.37 $\pm$ 1.26a	0.23 $\pm$ 0.19a	0.45 $\pm$ 0.08a	0.46
<i>Arbutus arizonica</i>	18.8 $\pm$ 1.9a	14 (26)	1926–2023	46 $\pm$ 19 ab	1.86 $\pm$ 0.55 ab	16.58 $\pm$ 7.31b	0.22 $\pm$ 0.13a	0.67 $\pm$ 0.10b	0.48

0.117), *J. deppeana* and *A. arizonica* ($r = 0.27$, $p = 0.087$) and *J. deppeana* and *Q. grisea* ($r = 0.30$, $p = 0.058$) (Fig. 4). In contrast, the highest correlation between species series corresponded to *P. engelmannii* and *Q. grisea* ($r = 0.44$, $p = 0.004$), followed by *P. engelmannii* and *A. arizonica* ($r = 0.38$, $p = 0.013$) and *Q. grisea* and *A. arizonica* ($r = 0.35$, $p = 0.024$). These results were also captured by the PCA, with the PC1 and PC2 accounting for 50.0% and 21.6% of total growth variability, respectively (Fig. S4). In the PCA biplot, years with low growth indices were clearly emphasized such as 1988, 1996, and 2011 (Figs. 4 and S4), whereas the highest growth indices corresponded to years 1997, 2010, and 2015.

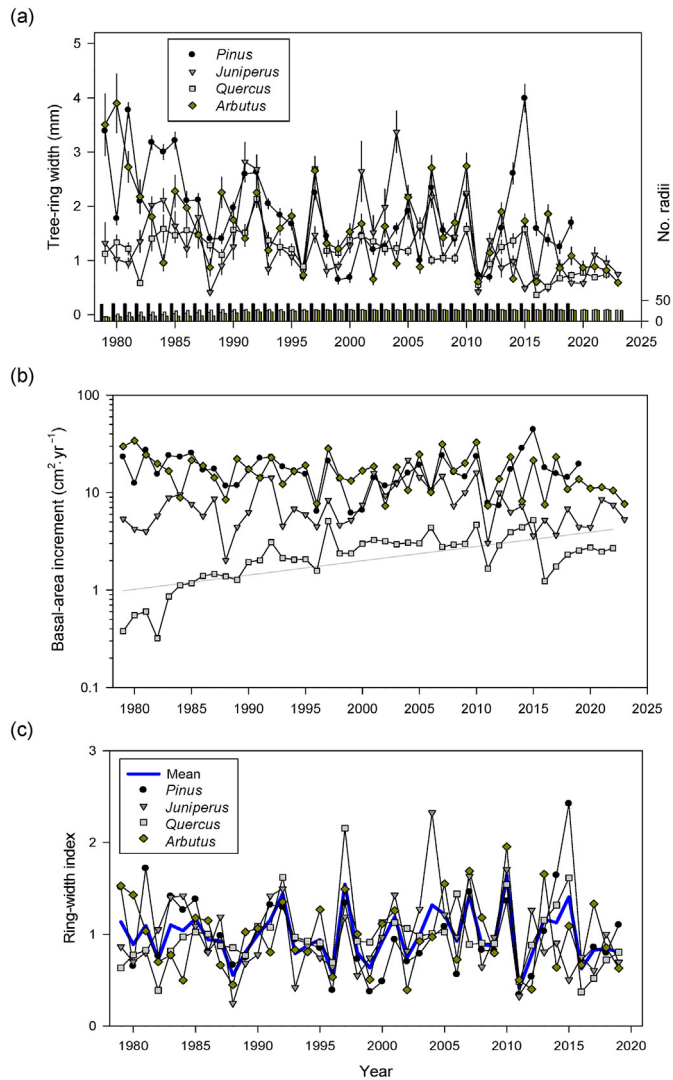


Fig. 4. Species series of (a) tree-ring width, (b) basal area increment, and (c) ring-width indices. In plot (a) values are means $\pm$ SE. In plot (b), the grey line shows the significant positive slope of *Quercus*. In plot (c), the blue line is the mean of the four species.

3.3. Growth responses to climate variables and teleconnection indices

Tree growth positively responded to daily precipitation, especially for *P. engelmannii* and *J. deppeana*, considering the climate window from prior autumn to current early spring (Table 2). The two broadleaves showed lower correlations, peaking later from late winter to late spring. All species showed negative correlations with temperature, being again strongest in absolute terms for the two conifers but peaking in winter-spring in the case of *J. deppeana* and then in spring-early summer in *P. engelmannii*. A similar climate window for temperature was also found for *A. arizonica*, but *Q. grisea* presented the earliest response from spring to early summer.

Considering monthly climate variables, the growth of the study species was enhanced by high precipitation from prior summer to current spring, particularly in the case of *P. engelmannii* and *J. deppeana* (Fig. 5). Elevated temperatures during the same period were negatively correlated with growth indices in *P. engelmannii*, whilst this was only observed in January and February in the case of *A. arizonica* and *J. deppeana*, respectively. In the case of minimum temperatures, a negative correlation was found in May with *P. engelmannii* growth indices. Wet conditions from previous November to current April improved *P. engelmannii* growth (Fig. S5).

The correlations with teleconnections indices showed negative responses from prior August to November and also in January with SOI in the case of *P. engelmannii* reaching a minimum value in January ($r = -0.52, p < 0.01$) (Fig. S6). In this species, positive correlations with El Niño 3.4 indices, peaking in February–March ($r = 0.41, p < 0.01$), and the PDO, were also found from prior August to current July, peaking in May–July ($r = 0.45, p < 0.01$), whereas *Q. grisea* showed positive correlations with June–July El Niño 3.4 indices ($r = 0.32, p < 0.05$). These associations were illustrated by positive correlations between *P. engelmannii* growth indices and SSTs in the Pacific Ocean in front of western México (110° – 120° W, 16° – 26° N; Fig. S7).

3.4. Growth responses to drought

Correlations between SPEI and the growth indices were maximum in *P. engelmannii* ($r = 0.72, p < 0.001$, September 13-month SPEI; Fig. S5), followed by *J. deppeana* ($r = 0.48, p < 0.001$, June 9-month SPEI; Fig. 6). In the broadleaves, correlations peaked earlier than in conifers, being higher in *Q. grisea* ($r = 0.46, p = 0.003$, April 2-month SPEI) than in *A. arizonica* ($r = 0.39, p = 0.01$, May 5-month SPEI; Fig. 6). Overall, *P. engelmannii* showed the highest responsiveness to drought, whilst the broadleaf *A. arizonica* showed the lowest responsiveness, despite both species presented high growth rates and earlier growth onset. On the other side, *J. deppeana* and *Q. grisea* showed intermediate responses to drought and were characterized by slower growth rates and later growth onset.

The SEA showed growth reductions due to drought in all species, but the growth drop was significant during dry years only in *P. engelmannii*, which showed a rapid recovery (Fig. 7). A similar finding was obtained when repeating the SEA based on non-overlapping severe drought years (1980, 1989, 1999, 2011 and 2017).

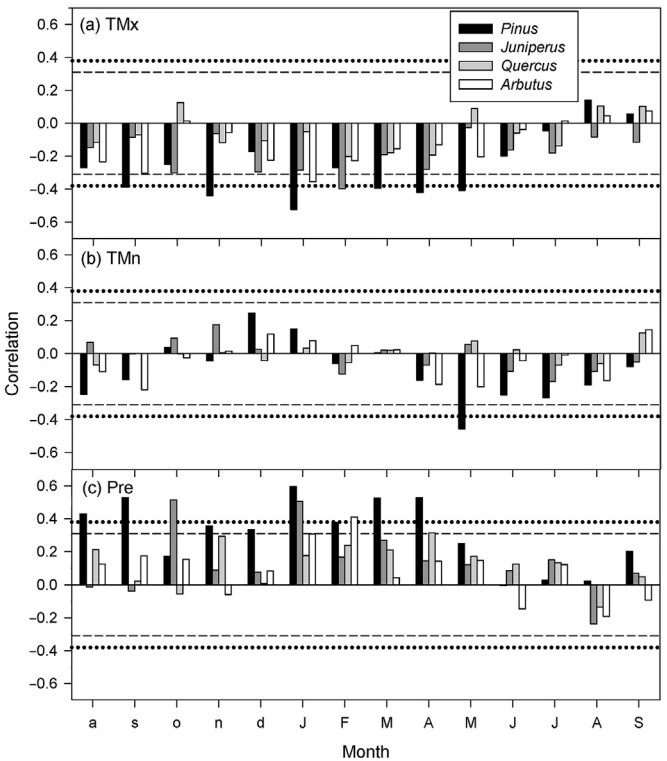


Fig. 5. Climate-growth relationships assessed by calculating Pearson correlations between species series of ring-width indices and monthly climate variables (TMx, mean maximum temperature; TMn, mean minimum temperature; Pre, total precipitation). The horizontal dashed and dotted lines correspond to the 0.05 and 0.01 significance levels, respectively.

3.5. Using the VS model to infer the climate drivers of growth

The calibration statistics showed that the VS model successfully predicted growth variability, particularly in the two conifers (Table 3, Fig. S8). According to the VS model, all species showed growth limitations due to elevated temperatures in summer, being stronger in the two conifers and *A. arizonica* (Fig. 8). Limitations due to insufficient soil moisture were found in late spring in the two conifers and also in *Q. grisea* and again in late summer and early autumn, particularly in *J. deppeana* and *A. arizonica*. Lastly, growth limitations due to low winter temperatures were also predicted for *A. arizonica* and *P. engelmannii*.

4. Discussion

Our results did not support the main hypothesis because early-growing species such as *P. engelmannii* and *A. arizonica* showed high and low growth responsiveness to drought, respectively. This study illustrated how to pinpoint the main climate drivers of growth in coexisting tree species using a battery of analyses. We showed that xylogenesis data are required to understand how climate extreme such as drought constrain cambial activity and wood formation, but they can be complemented by process-based growth models which allow inferring

Table 2
Statistics of climate-growth correlations calculated at daily scale.

Species	Precipitation		Temperature	
	Optimal selection	Highest Pearson correlation coefficient (date)	Optimal selection	Highest Pearson correlation coefficient (date)
<i>Pinus engelmannii</i>	Jan. 21 – March 21	0.65 (Jan. 22)	April 10 – June 8	–0.52 (April 9)
<i>Juniperus deppeana</i>	Oct. $t-1$ 4 – Dec $t-1$ 2	0.50 (Oct. $t-1$ 3)	Jan. 25 – March 25	–0.50 (Jan. 25)
<i>Quercus grisea</i>	March 24 – May 22	0.38 (Apr. 19)	April 24 – June 22	–0.36 (April 23)
<i>Arbutus arizonica</i>	Feb. 19 – April 20	0.46 (Feb. 20)	Jan. 29 – March 29	–0.41 (Jan. 29)

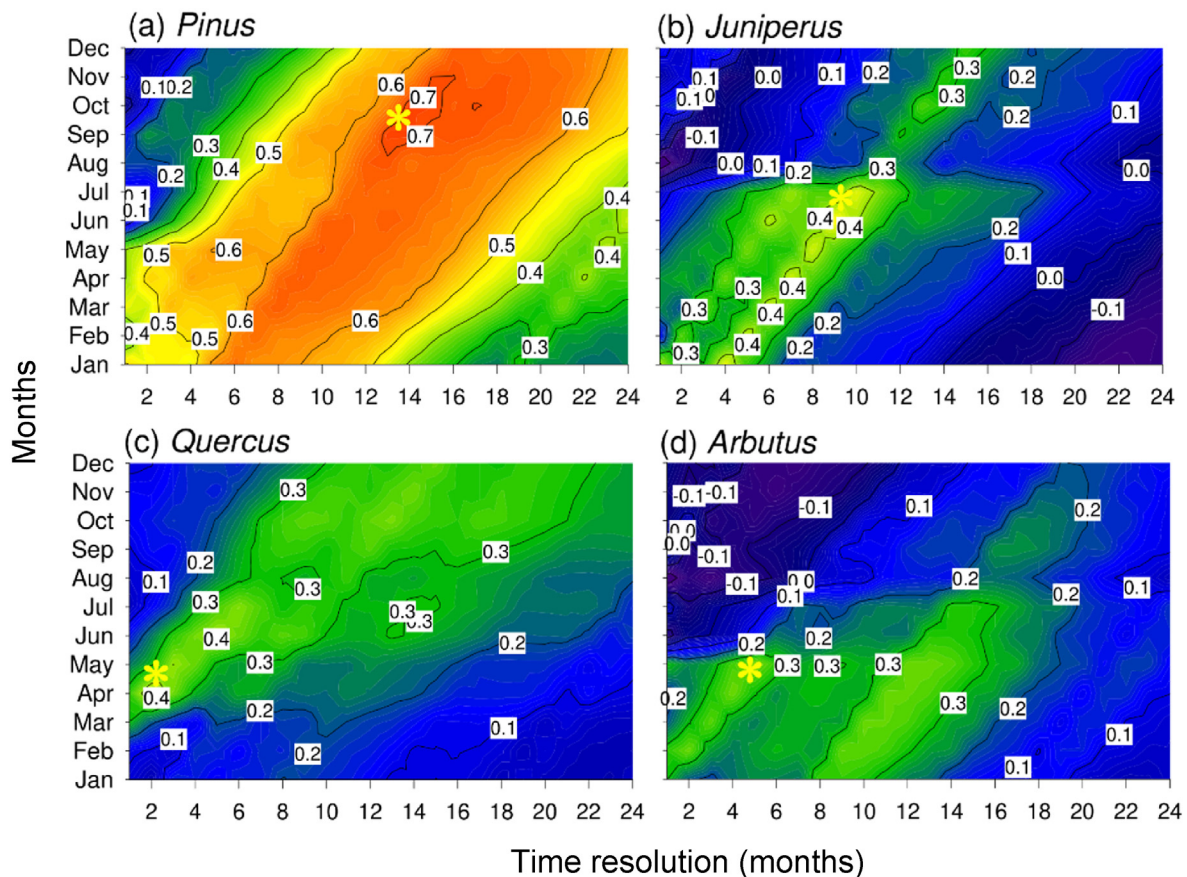


Fig. 6. Drought-growth relationships assessed by calculating Pearson correlations (color scale) between species series of ring-width indices and monthly SPEI values calculated at 1- to 24-month long scales (x axes). The yellow asterisks show the months and time resolution when correlations peaked.

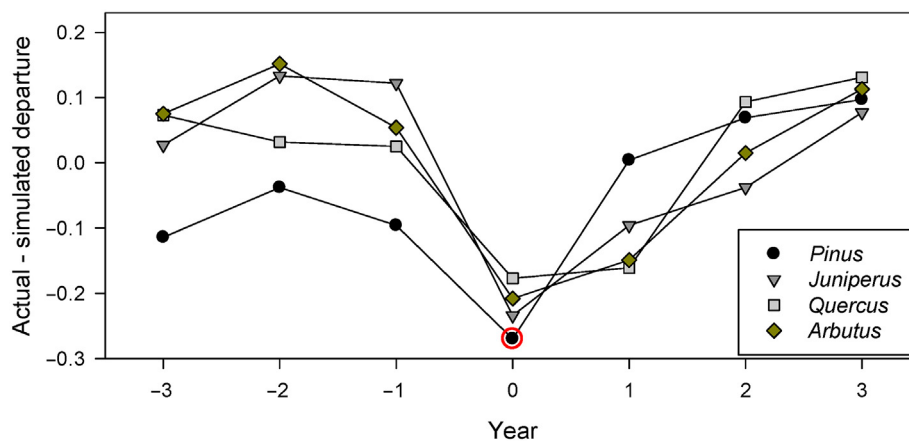


Fig. 7. Superposed epoch analysis comparing growth indices for drought years (year 0) and the three previous (−1 to −3) and subsequent (+1 to +3) years. Lines show mean values of actual minus simulated departures of ring-width indices for the four study species. The red symbol indicates a significant ($p < 0.05$) negative growth departure in *P. engelmannii*.

the main climate limitations of xylem production and forecasting growth variability under diverse climate scenarios (Tumajer et al., 2022; Valeriano et al., 2023a, 2023b).

In the study species, radial growth was constrained by low precipitation and elevated temperatures leading to higher evapotranspiration rates and drought stress. This was very noticeable in the two study conifers with responses to precipitation peaking earlier in *J. deppeana* which started forming radially-enlarging tracheids before *P. engelmannii*. In the broadleaves, the latest negative response to temperature was found

in *Q. grisea*, in agreement with its more delayed xylogenesis as compared with *A. arizonica*. These differences between species are important because temperature is a major triggering factor of the cambial onset in spring, but the final ring width depends on the turgor of cambial cells and the production of radially-enlarging cells (Horacek et al., 1999; Larson, 1994; Vaganov et al., 2006; Peters et al., 2021). Therefore, a more delayed production of radially-enlarging tracheids in *P. engelmannii* could allow this species rapidly growing using summer precipitation, but at the cost of facing dry spring conditions and drawing upon water reserves

Table 3

Statistics of the indexed ring-width series based on the VS model and considering calibration (1980–1999) and verification (2000–2019) periods. Statistics are Pearson correlation coefficient (r), root-mean-square error (RMSE), and Gleichläufigkeit (Glk).

Species	Period 1980–2019			Calibration (1980–1999)		Verification (2000–2019)	
	r	Glk (%)	RMSE	r	Glk (%)	r	Glk (%)
<i>Pinus engelmannii</i>	0.79	83	0.252	0.74	81	0.87	85
<i>Juniperus deppeana</i>	0.52	66	0.381	0.51	67	0.54	65
<i>Quercus grisea</i>	0.47	68	0.335	0.67	67	0.46	70
<i>Arbutus arizonica</i>	0.37	63	0.349	0.42	57	0.38	65

stored in the stem (Swidrak et al., 2011). This would explain the highest growth rates and responsiveness to drought and elevated temperatures of *P. engelmannii*. In the case of broadleaves, *A. arizonica* grew more and earlier and also showed higher sensitivity to changes in temperature and precipitation than *Q. grisea*.

In general, our results concur with other studies on Madrean mixed pine-oak forests which used tree-ring data and showed the importance of winter-spring precipitation for radial growth (González-Casares et al., 2017; Bickford et al., 2011). However, recent studies in these forests have also explicitly considered intra-annual growth patterns by performing xylogenesis analyses (Pompa-García et al., 2021, 2023a). They have revealed how earlywood production was enhanced by wet-cool conditions (low VPD) and latewood production positively responded to autumn temperatures (high VPD). Moreover, the seasonal sensitivity of *P. engelmannii* growth to drought also corresponded to changes in canopy greenness (Acosta-Hernández et al., 2024). These varying responses of intra-annual growth to precipitation and temperature, which impact soil moisture availability and VPD, could be compatible with bimodal growth patterns, already described in seasonally dry forests from the Mediterranean Basin (Camarero et al., 2010) and SW U.S.A. (Morino et al., 2021). The temporal pattern of radially-enlarging cells in *J. deppeana* suggests a bimodal growth behavior. Further studies should consider the role played by high VPD to constrain cell turgor and growth since this variable may increase as maximum temperatures rise and aridification progresses (Grossiord et al., 2020). For instance, in a tropical montane forest from SW China, a warmer and drier pre-monsoon season leading to high VPD delayed the onset of xylogenesis in broadleaf tree species and reduced radial growth (Liu et al., 2024). In addition to climate, intrinsic tree features can also affect xylogenesis and growth variability including tree age and size (Rossi et al., 2008). Here, we selected relatively young

trees of similar diameter. Therefore, we expect that the magnitude of this effect is minor.

Our results agree with other studies focusing on intra-annual growth patterns, but mainly carried out in subalpine and temperate conifer and mixed forests (Oberhuber and Gruber, 2010; Cuny et al., 2012; Michelot et al., 2012). For instance, using dendrometer data, it was found that elevated VPD and low soil water potential were the main climate constraints of growth in conifers and broadleaves, respectively (Etzold et al., 2022). This concurs with the higher growth limitation by warm conditions and low precipitation observed in the two study conifers. An earlier cambial reactivation has been observed in other pine species (Rossi et al., 2009). The decrease in pine growth rate early in the growing season could be linked to high below-ground demand for carbohydrates to ensure resource acquisition afterwards if conditions in the late growing season become drier (Oberhuber and Gruber, 2010). A longer growing season of pine species such as *Pinus sylvestris* than coexisting deciduous hardwood species has also been reported in temperate mixed forests (Cuny et al., 2012). In a similar temperate mixed forest, pine (*Pinus sylvestris*) growth began before the needles unfolded and there was no decrease in the concentration of non-structural carbohydrates (NSC) during the growing season suggesting a dependence on reserves assimilated the previous year, whilst oak (*Quercus petraea*) quickly formed earlywood before budburst and showed a subsequent starch decrease in the stem until early summer (Michelot et al., 2012). Therefore, seasonal changes in tissue NSC concentrations could be measured in pine and oak species from Madrean forests to test if this also occurs under summer-monsoon influence.

In temperate forests, growth peaked in the early growing season, commenced shortly before the summer solstice and occurred only during 30%–80% of days within the growth period (Etzold et al., 2022). Therefore, in these humid ecosystems the number of days with growth determined the final annual growth (Michelot et al., 2012), whereas in other studies carried out in sites with drier growing-season conditions growth rate was a more important factor controlling total growth (Cuny et al., 2012; Ren et al., 2019). Our situation is closer to the second case because the fast-growing species produced more radially-enlarging tracheids and wider earlywood, and they did it rapidly by leveraging the increase in soil moisture due to the summer rainfall. This dependence on monsoon summer is also corroborated by the strongest correlations of *P. engelmannii* growth indices with the PDO and the SSTs over the Pacific Ocean.

The study species showed different optimal climate windows and responses to drought at distinct temporal scales, which has been observed before (Pasho et al., 2012; Camarero et al., 2021). Conifers responded to longer droughts than broadleaves. The most responsive species showed

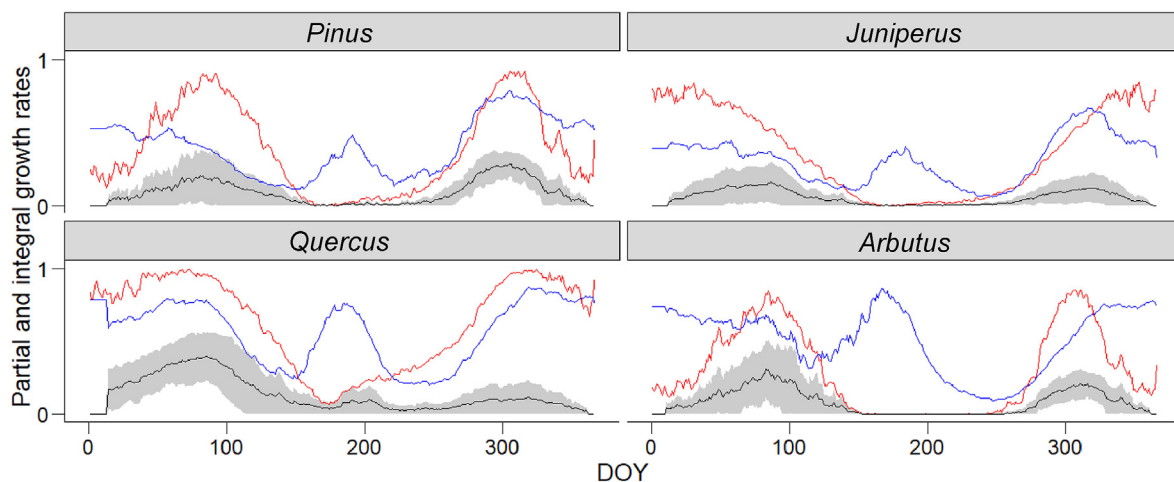


Fig. 8. Integral growth rates (black lines, means and standard deviations) and partial growth rates driven by soil moisture (GrW, blue lines) and air temperature (GrT, red lines) predicted by the VS model.

the strongest growth reduction during dry years, which suggests that post-drought growth resilience and growth sensitivity to drought are related (Schwarz et al., 2020; Serra-Maluquer et al., 2022). We focused on growth and xylogenesis, but drought impacts other aspects of wood formation usually leading to the production of tracheids or vessels with smaller lumen (Corcuera et al., 2004; Martín-Benito et al., 2013). These variables could be further analyzed in combination with NSCs to assess how growth depends on the balance between carbon sources and sinks or hydraulic conductivity.

It is challenging to predict which tree species will be more vulnerable to warmer and drier conditions based on our findings. It has been speculated that isohydric species such as *P. engelmannii* and *A. arizonica* may be at greater risk of death from depletion of carbohydrate reserves during prolonged drought, but altered hydraulic function has been more consistently reported during multi-year dry conditions (Anderegg et al., 2012). In addition, a higher vulnerability to drought stress has been reported in isohydric pines than in coexisting anisohydric junipers (e.g., Camarero et al., 2015), which form narrow conduits and are more resistant to xylem embolism. Nevertheless, die-off and strong mortality events in junipers have also been reported (Gazol et al., 2017; Camarero et al., 2020; Kannenberg et al., 2021). Our results show that the fast-growing *P. engelmannii* and *A. arizonica* were the most vulnerable, in terms of growth reduction, to precipitation decreases within the compared conifers and broadleaves. If conditions become drier in winter and spring, these two species could show stronger growth decline than *J. deppeana* or *Q. grisea*. Nonetheless, tree species show multiple strategies to recover after drought, either by mobilizing NSCs and water stored in the stem, by uptaking deep water sources (e.g., oaks) or through bimodal growth patterns (e.g., pines, *Arbutus*; cf. Camarero et al., 2010, 2021). These aspects could be explicitly incorporated in future studies on radial growth in seasonally dry environments.

5. Conclusions

The combination of intra- and inter-annual analyses of growth and the assessment of its responses to climate and drought at different temporal scales revealed different strategies to acclimate to hydroclimate variability of coexisting conifers and broadleaves. *P. engelmannii* and *A. arizonica* showed high growth rates and earlier growth onset, whereas *J. deppeana* and *Q. grisea* showed slower growth rates and later growth onset. The conifer *P. engelmannii* presented the highest responsiveness to drought, whilst the broadleaf *A. arizonica* showed the lowest responsiveness. Under warmer and more arid conditions characterized by more frequent and hotter winter-spring droughts, stands dominated by conifers such as *P. engelmannii* could shift towards mixed stands with presence of broadleaves such as oaks and *A. arizonica*. Therefore, drought timing is also relevant because late-growing species such as *J. deppeana* and *Q. grisea* would be more vulnerable to spring-summer droughts linked to the Monsoon than early-growing species such as *P. engelmannii* and *A. arizonica*. Our approach could be more widely used to better understand the underlying short-term processes (xylem phenology) of long-term growth responses to climate variability, particularly considering that these responses are usually not linear in the case of climate extremes such as droughts. Field monitoring of stem radius changes at fine temporal resolution (every 15–30 min) using automatic dendrometers is a promising research avenue to pinpoint the intra-annual and intra-daily growth responses to droughts of different severity and timing.

CRedit authorship contribution statement

Marín Pompa-García: Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **J. Julio Camarero:** Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Cristina**

Valeriano: Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis. **Eduardo Daniel Vivar-Vivar:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation.

Data availability

Data are available on reasonable request to the first author.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2025.100292>.

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