



Minimum and maximum wood density as proxies of water availability in two Mexican pine species coexisting in a seasonally dry area

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Abstract

Key message Minimum wood density is a proxy of soil moisture during the early growing season. Maximum wood density responds to late growing-season drought.

Abstract Seasonally dry areas are ideal settings to refine our understanding of tree growth proxies of water availability. Despite recent methodological advances in quantitative wood anatomy and wood density, our knowledge of wood density responses to climate at intra-annual scales in seasonal drought-prone regions is still limited. The objective of this study is to elucidate how minimum (MnD) and maximum (MxD) wood density respond to hydroclimate variability of two coexisting conifers growing in a moisture-stressed environment. We prepared wood samples to obtain MnD and MxD values in *Pinus lumholtzii* and *Pinus durangensis* trees co-occurring in a drought-prone site located in northern Mexico. MnD and MxD were correlated with temperature, water balance and a drought index considering the period 1970–2013. The *P. lumholtzii* MnD negatively responded to growing-season water availability as indicated by the negative correlations with water balance, and considering short to mid-term droughts lasting from 2 to 8 months. Both species showed a decrease in MxD during the last 15 years associated to a rise in temperature and drier conditions. Winter-spring water balance was positively associated with MxD, but July water balance showed a negative correlation. Intra-annual density data can represent robust proxies of hydroclimate variability in similar seasonally dry areas. Specifically, MnD should be further investigated as a surrogate of water availability effects on earlywood during the early growing season.

Keywords Dendroecology · Drought · Hydroclimate · Mexico · Wood density

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Introduction

Given the threat of forest dieback and growth decline in seasonally dry regions (Allen et al. 2015), the scientific community is concerned with improving our knowledge on the ecological and climatic constraints that trees face when stressed by drought (Brodribb et al. 2020). Tree rings constitute natural records of hydroclimate variability as documented by dendrochronological studies (Fritts 2001). As annual tree rings often have seasonal growth bands, there is the potential to capture seasonally resolved climate information. For example, the separate measurements of earlywood and latewood expand and improve the capabilities to understand climate-growth associations and link them to tree-ring formation (Griffin et al. 2013; Torbenson et al. 2016). The dense latewood provides mechanical support and the less dense earlywood is important for the tree hydraulic conductivity (Björklund et al. 2017). At long time scales, latewood density reflects changes in summer temperatures (Rathgeber

2017). These different functions and couplings with climate are reflected in changes in wood density between and within tree species (Muller-Landau 2004).

Intra-annual changes in wood density along the ring are proxies of tree growth responses to hydroclimate (De Micco et al. 2019; Camarero and Hevia 2020). In particular, changes in minimum (hereafter MnD) and maximum (hereafter MxD) wood density, which are tightly related to earlywood and latewood density, respectively, reveal how climate affects wood formation, i.e. the size and number of tracheids produced (Camarero et al. 2014; Belokopytova et al. 2019). In the case of a growth reduction due to insufficient water availability, wood density changes may reflect drought stress because trees react by forming more narrow conduits and a more dense wood during the early growing season (Martinez-Meier et al. 2008; Britez et al. 2014; Camarero et al. 2014; Schuldt et al. 2016). Changes in wood density may depend on xylogenesis and the moments when earlywood and latewood production occur, and on the coupling or decoupling with climatic and edaphic factors (Bouriaud et al. 2005). There is also a high variability between and within tree species in the responses of wood density to climate, which requires better quantification (Nabais et al. 2018). Furthermore, investigating how MnD and MxD are related by testing if they follow allometric relationships would improve our understanding of their responses to climate. For instance, it would allow discerning if MnD and MxD follow allometric associations as a function of declining water availability, i.e. how proportional is the increase of MxD as MnD. Regions where droughts impact growth and wood density of coexisting tree species provide valuable settings to answer these questions. In forested and seasonally drought-prone regions as northern Mexico and the Mediterranean Basin, tree radial growth is negatively impacted by drought (Camarero et al. 2014, 2017; González-Cásares et al. 2017; Pompa-García et al. 2018), but how seasonal wood density responds to changes in water availability is unknown.

There is a significant lack of knowledge about the potential of MnD and MxD as moisture proxies in seasonally dry regions, including northern Mexico, a hotspot of conifer diversity. If the MnD and MxD values differ between coexisting species and their responses to hydroclimate are also different, these differences would also imply changes in carbon content and storage and biomass production in mixed stands (Zeller et al. 2017). In xeric sites from northern Mexico MxD increased as water availability did (Pompa-García and Venegas-Gonzalez 2016), whilst in wet high-elevation *Pinus hartwegii* forests from central Mexico MnD positively responded to temperature (Correa-Díaz et al. 2020). An analysis of the relationships between radial growth, wood density and hydroclimate is therefore crucial to anticipate changes of productivity and carbon uptake in response to

drought, and even extinction risks of maladapted species or populations (Allen et al. 2015). Hydroclimate drives growth by affecting the number of produced tracheids and drives wood density by influencing the lumen and cell-wall thickness of tracheids (Rathgeber 2017).

According to Camarero and Gutiérrez (2017), dryness during the growing season leads to MnD changes in conifers from xeric sites. Conifers in such dry sites produce dense earlywood characterized by narrower tracheid lumens in response to precipitation shortage during early spring leading to higher MnD values, whilst MxD is related to changes in summer temperature and precipitation (Camarero and Hevia 2020; Camarero et al. 2017). Classically, MxD has been regarded as a strong proxy of summer temperatures in cold regions (Björklund et al. 2017), but how MxD and MnD respond to changes in water availability is still understudied (cf. Rathgeber 2017).

Here, we focus on *Pinus lumholtzii* and *Pinus durangensis*, two pine species with dendrochronological potential (Pompa-García et al. 2015; González-Cásares et al. 2017), widely distributed in northern Mexico where they have a great economic importance for local people (González-Elizondo et al. 2012). We aimed to test if MnD and MxD of these two species respond to hydroclimate variability during the growing season in northern Mexico. We hypothesize that MnD and MxD will show responses to dry conditions during the early and late growing seasons, respectively. Specifically, we expect that MnD will increase in response to low growing-season water availability inducing the formation of earlywood tracheids with narrow lumen. We also expect a positive response of MxD to increased water availability leading to a longer growing season and the production of more latewood.

Materials and methods

Study site, tree species and field sampling

Stem wood samples were collected from *P. lumholtzii* and *P. durangensis* trees growing at a site in Sierra Madre Occidental (27° 04' 35" N, 107° 08' 20" W, 1390 m a.s.l.), northern Mexico (see Fig. S1, Supplementary Material). The mean site slope is 3%, the mean crown cover 60% and the mean standing volume 70 m³ ha⁻¹ (González-Cásares et al. 2017). The vegetation is formed by mixed pine and oak–pine forests with junipers and other shrubs (González-Elizondo et al. 2012). According to local, short meteorological records from the nearby Guachochi station (26° 50' N, 107° 05' W, 2420 m a.s.l.) the climate in the study area is temperate with dry winters and hot but wet summers. The mean temperature is 16.2 °C and annual precipitation sum is 779 mm (period 1970–2005), with 46% of this precipitation falling from July

to August (INEGI 2005). Summer precipitation depends on the activity of the North American monsoon (Adams and Comrie 1997). Soils are Regosols and Leptosols of volcanic origin.

In this area, *P. lumholtzii* inhabits dry sites with semi-arid climate conditions from 1200 to 2900 m on rocky and shallow soils with low water-holding capacity, whereas *P. durangensis* is mainly distributed at an altitudinal range of 1300–3000 m mixed with fir species in wet, high-elevation sites (González-Elizondo et al. 2012). There are previous dendrochronological studies on both species in northern Mexico (Villanueva-Díaz et al. 2000, 2006).

We sampled from 7 to 10 dominant trees for each species. The mean diameter at 1.3 m of sampled *P. durangensis* and *P. lumholtzii* trees were 44.5 cm and 36.0 cm, respectively, whereas their mean heights were 22.0 m and 12.0 m, in that order. One 10-mm core per tree was extracted at 1.3 m using a Pressler increment borer. These trees were previously cored and their tree-ring width series were measured, cross-dated and presented by González-Cásares et al. (2017).

Climate data and drought index

Since local climate data are missing and heterogeneous in the study area, we obtained mean maximum (TM_x) and minimum (TM_n) and total precipitation (P) at a monthly scale from the 0.5°-gridded CRU TS 4.03 climate database (Harris et al. 2020). We also calculated the potential evapotranspiration (PET) following Hargreaves and Samani (1982) to obtain the monthly climate water balance as the difference between precipitation and PET (P–PET). To quantify drought stress we used monthly values of the Standardized Precipitation-Evapotranspiration Index (SPEI) for 1–20 month long scales, i.e. calculated for the past 1–20 months. The SPEI considers the effect of temperatures on the evapotranspiration rate, with negative and positive SPEI values reflecting dry and wet conditions, respectively (Vicente-Serrano et al. 2010). Climate and SPEI data were downloaded for the grid with coordinates 107.0–107.5° W and 27.0–27.5° N using the Climate Explorer webpage (<https://climexp.knmi.nl>).

Tree-ring and X-ray microdensitometry analysis

Wood samples were cut using a double-blade circular saw (AFUME, France). Thin strips of approximately 1.3 mm thickness were obtained and resin was removed by refluxing strips in ethanol (96%) after a 24 h Soxhlet extraction. Wooden extracted laths were kept under constant temperature and humidity in the CETEMAS (Siero, Spain) microdensitometry laboratory, before being X-ray scanned in an Itrax Multiscanner (Cox Analytical Systems, Sweden). The samples were exposed to 30 kV, 50 mA for 25 ms in the

radial direction (20- μ m step size) using a Cu tube. Wood density profiles were obtained for each sample using WinDendro (Regent Instruments, Québec, QC, Canada). The measured ring-width series of radiographic images were visually cross-dated, and compared with chronologies published by González-Cásares et al. (2017).

Minimum and maximum wood density values per tree ring (in g cm⁻³) were extracted from the radiographic images (see Fig. S2, Supplementary Material) by calibrating the grey-scale intensities using a light calibration curve derived from a calibration step-wedge (Schweingruber 1996). A final check of the visual cross-dating based on tree-ring widths was carried out on these samples by using the COFECHA software (Holmes 1983). This yielded a total sample size of measured and cross-dated samples corresponding to five trees per species. Note that we considered MnD and MxD because: (i) they do not depend on the definition of the early-wood/latewood boundary as earlywood and latewood density do, and (ii) MnD has shown a stronger response to climate than earlywood density (Camarero et al. 2014, 2017). MnD and MxD correspond to the lowest and highest density values along the density profile of a tree-ring, respectively,

Processing density chronologies

The MnD and MxD series were subjected to detrending and standardization to remove long-term trends and to retain the year-to-year variability (Cook and Kairiukstis 1990). These procedures allowed calculating mean chronologies for each variable and species. First, we applied a power transformation to the individual density series to reduce heteroscedasticity. Second, a smoothing spline with a 50% frequency response at a wavelength of 2/3 of the series length was fitted to individual series since sampled trees presented similar ages (80–102 years). Then, MnD and MxD indices were obtained by subtracting the fitted curve from the observed values. The MnD and MxD indices were subjected to autoregressive modeling to remove autocorrelation for each individual trees. Then, they were averaged per species on a yearly basis using a bi-weight robust mean to produce mean series of pre-whitened indices or residual chronologies for each species (Fritts 2001). These procedures were performed using the ARSTAN v 4.4 software (Cook and Krusic 2007).

Statistical analyses

First, to understand how MnD and MxD values are associated in each species at the ring level, we followed an allometric approach by relating values of both variables measured for each individual ring and tree. We quantified the proportionality in the MnD–MxD relationships to assess if each species differently responded to climate, for instance by increasing more or less MxD as MnD

increases due to drought stress. We fitted Reduced Major Axis (RMA) regressions between MnD and MxD values because these variables showed associated variation due to both measurement and sampling errors (Sokal and Rohlf 1995). To compare the slopes of MnD-MxD RMA regressions between the two species, we calculated confidence intervals following Warton et al. (2006). The heterogeneity of regression slopes was assessed using analysis of variance and post hoc Tukey tests. The parameters fitted were calculated using the SMATR software (Falster et al. 2006). We calculated 95% bootstrapped confidence intervals for the slopes and intercepts based on 9999 replicates using the software PAST ver. 3.0 (Hammer et al. 2001). Lastly, comparisons between mean MnD and MxD values were done using Student *t* tests after checking for normality. The following RMA regressions relating MnD (*x*) and MxD (*y*) were fitted to the two species: *P. durangensis*, $y = -1.831 + 5.536x$, $r = 0.255$, $p = 0.0005$, $n = 191$; *P. lumholtzii*, $y = -1.133 + 4.285x$, $r = 0.274$, $p = 0.0001$, $n = 164$ (Fig. 1).

Second, to characterize the climate- and drought-density associations, both individual and mean series (residual chronologies) of MnD and MxD of each species were correlated with monthly climate variables (TMx, TMn, water balance) using Pearson correlations for the period 1970–2013. Before correlation analysis, autoregressive modelling was also applied on the climate data. Correlations were calculated from prior August to current September since most latewood is formed in early autumn (Pompa-García, pers. observ.). In the case of the SPEI, we calculated correlations from January to December and considering 1–20-month resolutions.

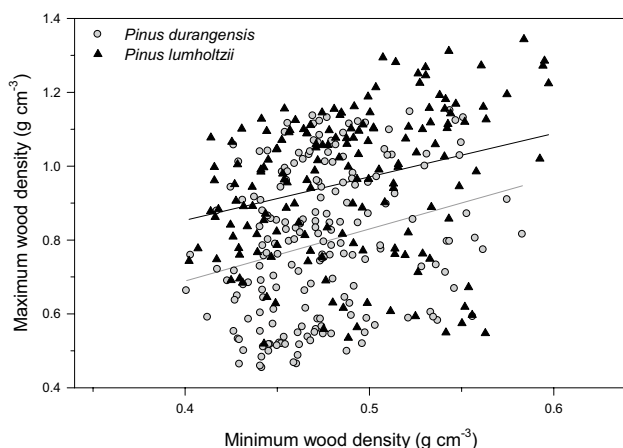


Fig. 1 Relationships between minimum and maximum wood density measured for individual rings in the two study pine species. The lines correspond to RMA regressions

Results

Patterns and associations between MnD and MxD

On average, and considering the common 1970–2013 period, *P. lumholtzii* had a higher absolute MxD (mean \pm SE = 0.95 ± 0.014 g cm⁻³) than *P. durangensis* (0.80 ± 0.013 g cm⁻³; $t = 7.94$, $p < 0.001$), while MnD was higher in *P. durangensis* (0.49 ± 0.004 g cm⁻³) than in *P. lumholtzii* (0.45 ± 0.004 g cm⁻³; $t = 5.59$, $p < 0.001$) (Figs. 1 and 2). The mean ring width did not significantly differ between the two species (*P. lumholtzii*, 1.47 ± 0.15 mm; *P. durangensis*, 1.35 ± 0.10 mm). The MxD series of both species were significantly correlated ($r = 0.70$, $p < 0.001$). In the case of *P. lumholtzii*, the MnD and MxD series were negatively related ($r = -0.32$, $p = 0.03$).

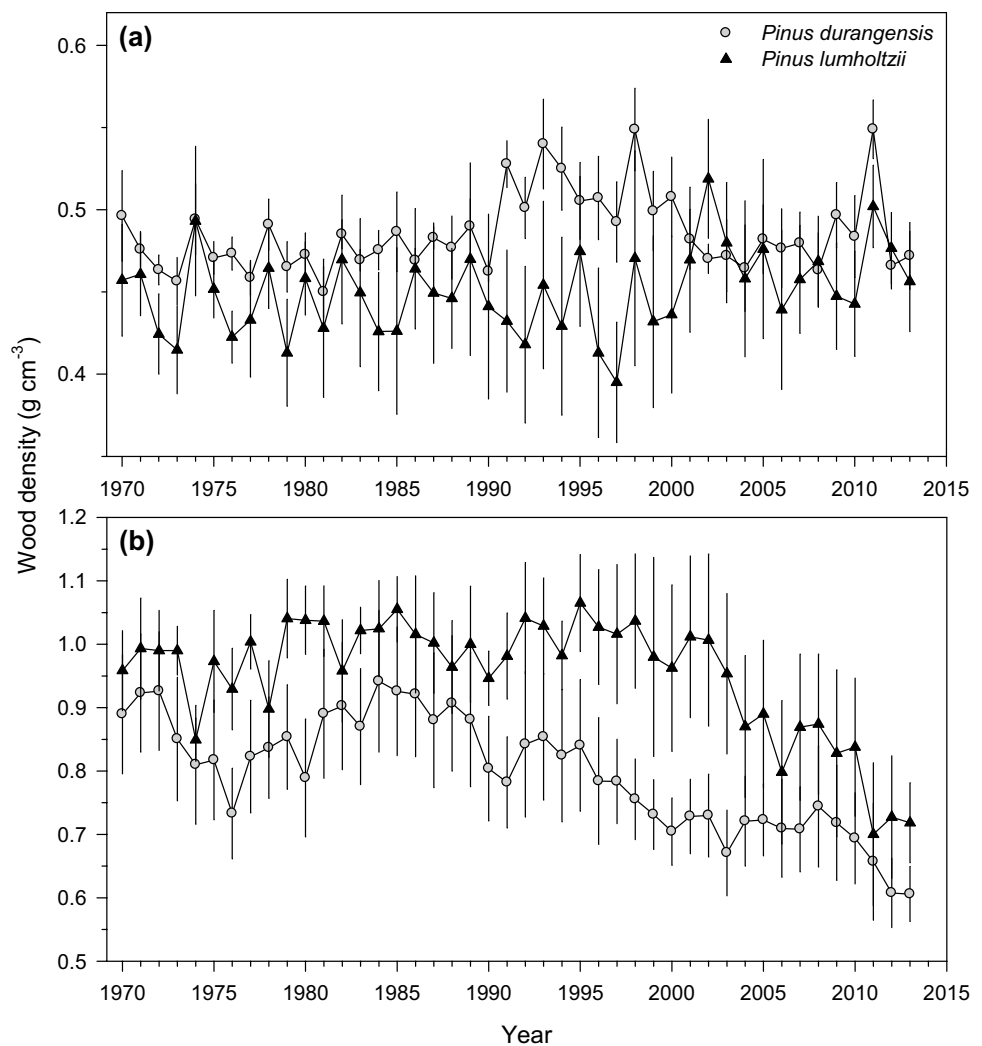
According to the 95% bootstrapped confidence intervals of the slopes for *P. durangensis* (4.744, 6.209) and *P. lumholtzii* (3.773, 4.731), the first species presented a significantly ($p < 0.05$) higher slope (Fig. 1).

The raw wood density series of both species showed a clear inter-annual variability with lower coefficient of variation in MnD (5–7%) than in MxD series (10–12%). The MnD series of *P. lumholtzii* showed a significant ($p < 0.001$) and positive slope (0.002) (Fig. 2a; slope not shown), whilst both species showed significant and negative MxD trends (*P. durangensis*, -0.005 ; *P. lumholtzii*, -0.004) (Fig. 2b; slopes not shown). The drop in MxD was very distinct in both species after 1995, when temperatures increased in the study area (Fig. S1). This reduction of MxD after 1995 corresponded to mean slopes of -0.008 and -0.019 in *P. durangensis* and *P. lumholtzii*, respectively (Fig. 2b; slopes not shown).

Associations of MnD and MxD with climate variables and the SPEI drought index

Several drought events (e.g., 1995, 1998, 2002–2003; see Fig. S1) coincided with sharp increases in MnD, particularly in *P. lumholtzii* (Fig. 2a). This explains why the MnD of this species was positively and significantly related to April and June TMx ($r = 0.37$ in both cases), but negatively related to the water balance in April ($r = -0.33$) and June ($r = -0.43$), and also in the previous summer (Fig. 3). Similar correlations were observed, albeit weaker, for *P. durangensis* MnD with June TMx ($r = 0.32$) and April water balance, respectively. Correlations for *P. durangensis* were mostly not significant. Regarding MxD, we again found stronger correlations for *P. lumholtzii* than for *P. durangensis*, with positive associations with

Fig. 2 Mean values of minimum (a) and maximum (b) wood density for the two study pine species. Values are means and error bars are standard errors



the prior winter (December and February) water balance, and during the early growing season (April; $r = 0.39$ in the case of *P. lumholtzii*), but negative correlations with July water balance (Fig. 4). TMx and MxD were negatively related from March to June (correlations ranging from $r = -0.37$ to $r = -0.50$). These negative associations were also observed for TMn and MxD from March to June ($r = -0.52$) in both species, and additionally from July to September in *P. durangensis*. In these analyses, most correlations between climate data and MxD and MnD series of individual trees were not significant ($p > 0.05$).

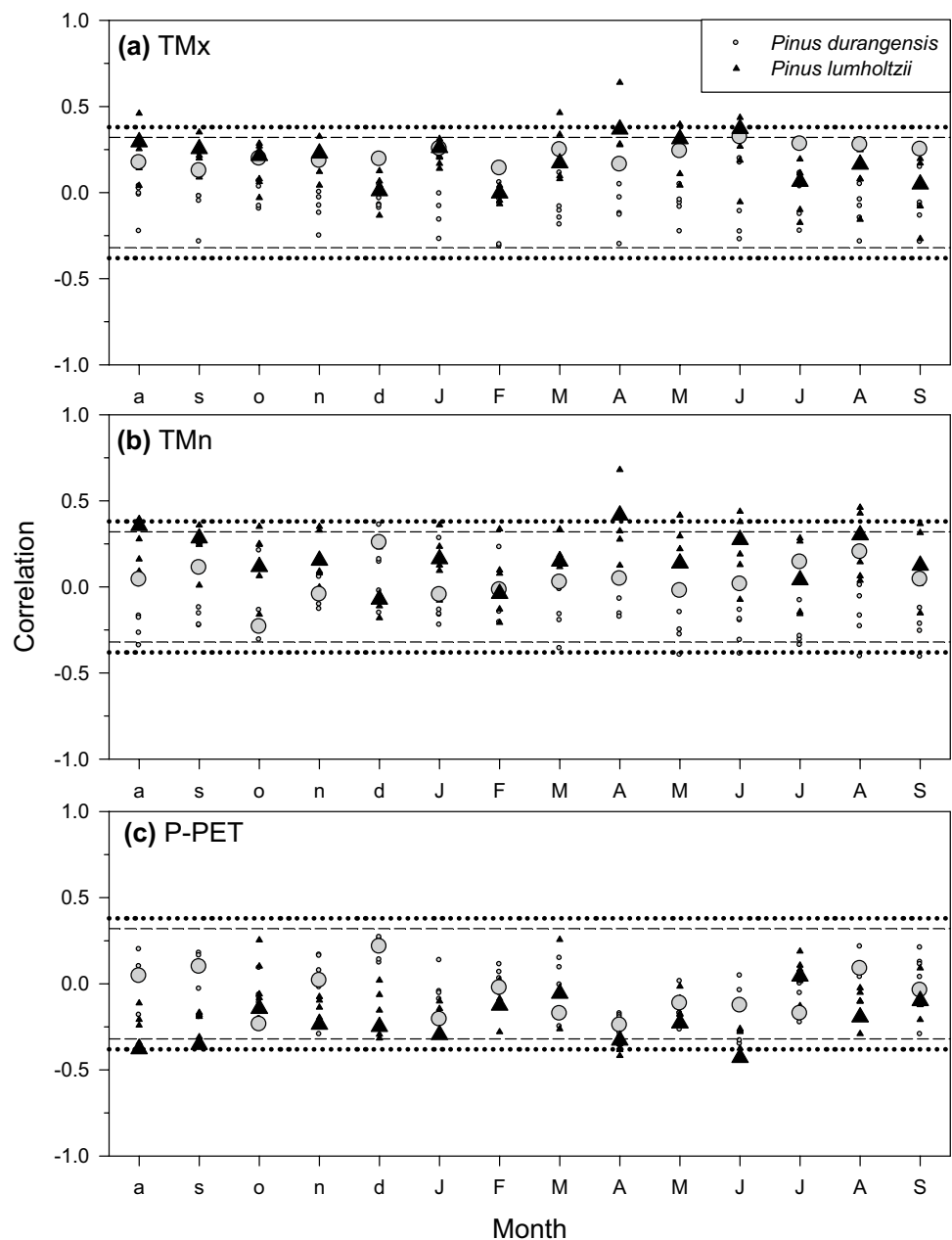
Similar to correlations with temperature and water balance, *P. lumholtzii* MnD was the most sensitive variable to changes in the SPEI drought index (Fig. 5). Wet conditions (high SPEI values) from May to July and at 2–8-month long scales were associated with low MnD values in this species. A similar, but again weaker, negative signal was observed between *P. durangensis* MnD and SPEI from July to October at 4–10-month resolution. With regard to MxD, negative correlations were found for *P. lumholtzii* during the late

growing season (July to December) and at short temporal scales (1–8 months). In *P. durangensis* MxD the negative signal was weak and found at 1-month scales in July, whilst positive correlations were detected in May–June at all temporal scales considered (1–20 months), and for all months at long scales (12–20 months).

Discussion

Our findings support the hypotheses concerning MnD and MxD responses to changes in water availability. As expected, MnD responded to changes in the hydroclimate conditions during the early growing season, which is in line with previous research in other conifers from xeric sites (Camarero et al. 2014; Camarero and Gutiérrez 2017). The signal of *P. lumholtzii* was stronger than for *P. durangensis*, and the *P. lumholtzii* MnD was the most robust and meaningful proxy of water availability during the growing season. This agrees with previous studies in conifers from xeric sites observing

Fig. 3 Relationships observed between indexed series of minimum wood density (MnD) in the two sampled pine species and monthly climate variables. The plots show the Pearson correlations calculated between minimum wood density for individual trees (small symbols) and **a** mean maximum temperature (TMx), **b** mean minimum temperature (TMn), and **c** water balance (P-PET). Correlations were calculated from prior August up to current September with months of the previous and current years abbreviated with lowercase and uppercase letters, respectively. Dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively

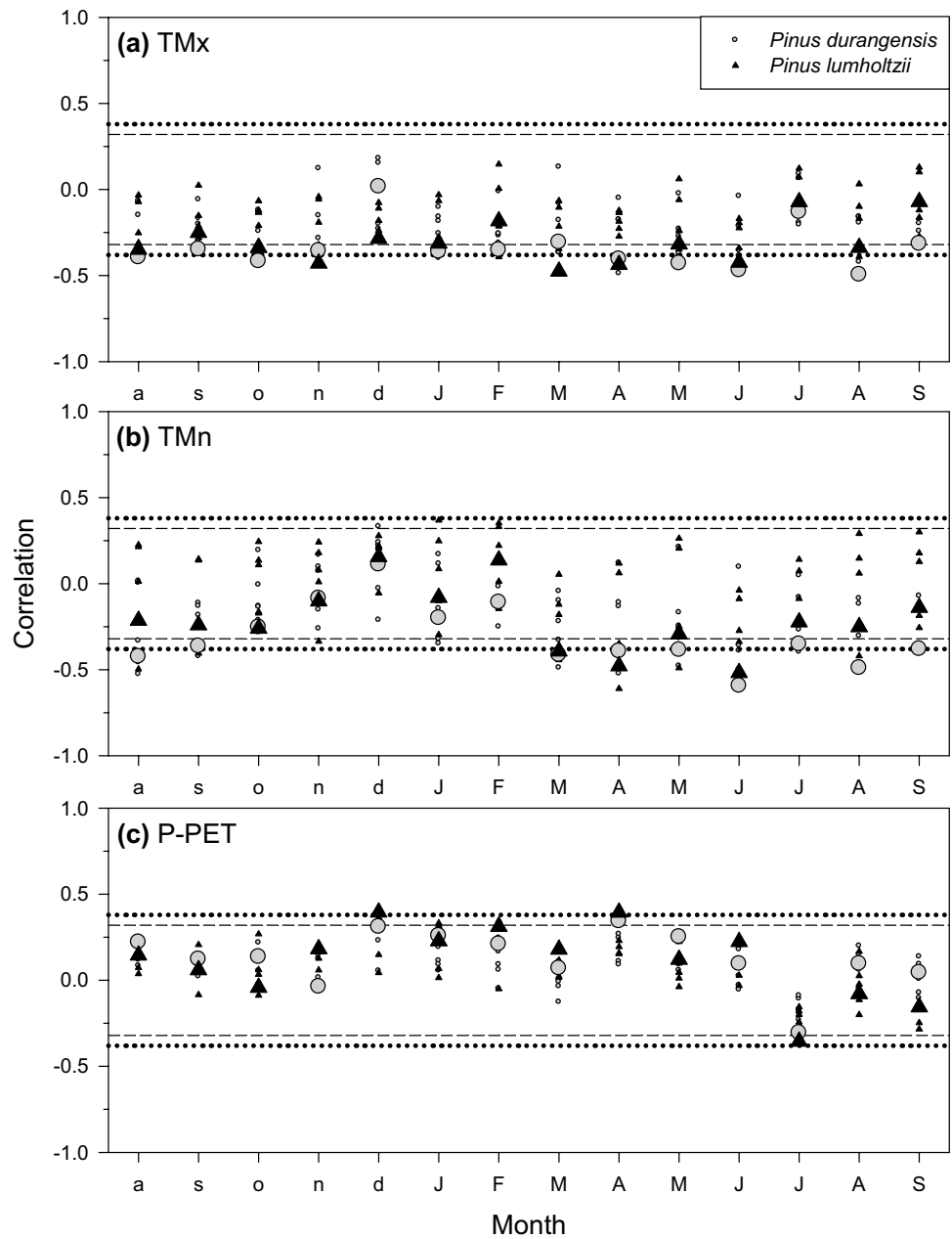


that changes in MnD reflect changes in water availability because dry conditions during the early growing season lead to the formation of tracheids with narrow lumen (Bouriaud et al. 2005) and a dense earlywood associated to reduced conductivity, higher MnD and a decrease in radial growth (Cleaveland 1986; Camarero et al. 2017; Camarero and Hevia 2020). Smaller cells with thicker walls due to little turgor pressure are formed under drought, whilst larger cells with thinner walls are developed in response to higher water availability (Björklund et al. 2017). Dry-warm conditions during the year prior to tree-ring formation could also contribute to reduce spring growth rate and increase MnD (Vaganov et al. 2006). As we show here and as Rathgeber

(2017) stated, MnD is still an understudied parameter of growth performance in drought-prone areas despite its ecological meaning. The morphology of earlywood tracheids determines MnD and the earlywood constitutes most of the annual ring growth (ca. 60–80%), and accounts for most of the hydraulic conductivity (Domec and Gartner 2002).

Regarding MxD, the positive associations with winter to spring water balance are similar to those found with ring width indicating improved growth conditions (wider rings; cf. González-Cásares et al. 2017), and the production of a thicker and dense latewood due to improved photosynthesis and more available carbohydrates. These associations are interesting because reflect extended influences

Fig. 4 Relationships observed between indexed series of maximum wood density (MxD) and monthly climate variables. The plots show the Pearson correlations calculated between maximum wood density for individual trees (small symbols) and mean species series (big symbols) and **a** mean maximum temperature (TMx), **b** mean minimum temperature (TMn), and **c** water balance (P-PET). Correlations were calculated from prior August up to current September with months of the previous and current years abbreviated with lowercase and uppercase letters, respectively. Dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively

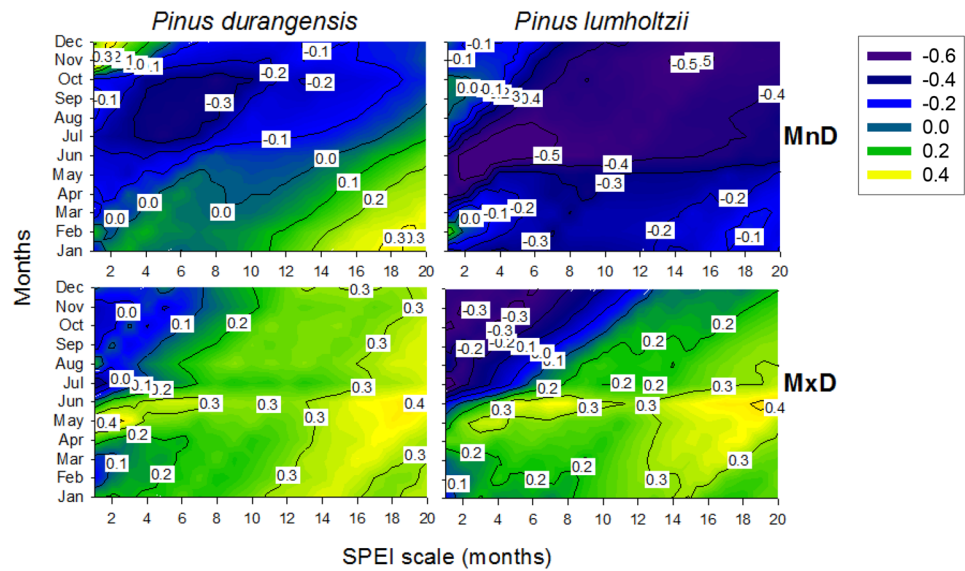


of climate on cell production (radial growth) and changes in cell morphology (density) despite growth and tracheid development (lignification and maturation) are lagged processes (Cuny et al. 2014). However, the negative association with summer water balance, which does not affect growth in these species (cf. González-Cásares et al. 2017), indicates the formation of latewood composed by tracheids with wide lumen and thin walls. This is a different response from the formation of narrow latewood, corresponding to the production of less cells, in response to dry summer conditions in the monsoonal North America (Griffin et al. 2013). Further research is needed to disentangle the responses of seasonal wood formation (reflecting cell

number) and wood density (reflecting cell morphology) to hydroclimate in seasonally dry sites.

It is also remarkable that this is the first research to analyze wood density responses to climate of two co-occurring pine species. In both species, MnD and MxD values of individual years were highly correlated. The higher MnD-MxD slope of *P. durangensis* implies that MnD increases more rapidly as MxD does than in the case of *P. lumholtzii*. In a previous tree-ring study, both species showed similar growth rates, but *P. lumholtzii* presented a much higher coherence in growth between trees in agreement with its higher growth responsiveness to climate (González-Cásares et al. 2017). These authors found that radial growth of both species was

Fig. 5 Drought-density associations based on the correlations calculated between the SPEI drought index and minimum (MnD) and maximum (MxD) wood density of the two study species. Correlations (color scale) were calculated considering 1- to 20-month resolutions (x axes) and from January to December (y axes). Significant correlations at the 0.05 level correspond to $r > 0.30$ or $r < -0.30$



enhanced by cool and wet conditions in the prior winter. This indicates that the climate-growth association of the tree-ring width was more lagged than the climate-MnD association, which was significant in spring when growth rates are assumed to peak. However, the climate-MxD association was significant in summer (July) when latewood formation should occur. Xylogenesis studies would be needed to investigate if these correlations are representing causal relationships.

Deciphering climate factors limiting wood density improves our understanding of the adaptive capacity of species to ongoing climate change because it is a surrogate of water availability during the growing season in seasonally dry sites (Arzac et al. 2018). Our results demonstrate that MnD is a robust proxy of hydroclimate and improves the understanding on how moisture fluctuations drive intra-annual wood formation. The climate-density associations, as the positive response of MxD to spring water balance, match with climate-growth associations investigated in similar species from dry areas (Pompa-García and Venegas-González 2016; González-Cásares et al. 2019a, b, c). These coincidences confirm the consistency in tree-growth responsiveness to climate in semi-arid regions (Fritts 2001). The higher responsiveness of *P. lumholtzii* MnD to drought (SPEI) throughout the year is in line with the fact that it is dominant in harsh, low-productivity dry sites (González-Elizondo et al. 2012), whereas *P. durangensis* is more abundant in more mesic sites and its MnD showed a lower responsiveness to growing-season drought. The response to drought was stronger (higher correlation coefficients in absolute terms) in *P. lumholtzii* than in *P. durangensis*. The stronger climatic signal of *P. lumholtzii* is coherent with its habitat and climate suitability since it is able to inhabit drier sites than *P. durangensis*.

Consequently, the studied co-occurring pine species will respond differently to forecasted drought conditions in northern Mexico (Seager et al. 2009). For instance, a marked decreasing trend for MxD after 1995 was found for both species, being more accentuated for *P. lumholtzii*. This negative tendency coincided with an increase in temperatures, particularly during dry months (see Stahle et al. 2016; Pompa-García et al. 2018). This is in line with previous findings that demonstrate that wood density of northern Mexico conifers is sensitive to high temperatures (González-Cásares et al. 2019b).

There is ample evidence of increasing spring temperature and decreasing trends of precipitation in the nearby SW USA over the last years (Williams et al. 2012). Such aridification trend and the increase in drought stress could reduce growth and MxD, thus decreasing carbon fixation in wood and forest productivity, and make pine wood less durable and resistant against fungi and other decomposers. Further research could investigate if the amount of carbon allocated to tracheid and cell wall formation differs between earlywood and latewood, or if changes in water availability mainly affect lumen size by influencing turgor pressure during tracheid enlargement and maturation.

Our results are also supported by previous analyses on drought effects on conifer wood anatomy showing a decrease in tracheid expansion during the early growing season and a reduced radial growth (Eilmann et al. 2009; Bryukhanova and Fonti 2013; Belokopytova et al. 2019). Importantly, density variables may have a stronger, more temporally stable and biologically founded response to hydroclimate than tree-ring width because they capture changes in wood anatomy (Camarero and Hevia 2020). Our results focused on comparisons between the two coexisting species, which limits extrapolation to regional and population scales. However,

the present results show different density responses to climate indicating adaptation of the two species to prevalent local climatic conditions. Nevertheless, our inferences are very limited due to sampling only five mature trees per species. This was evidenced by the correlations between density and climate for individual trees, which showed a high intra-specific variability. This individual variability should be also considered in addition to the species-specific responsiveness of wood density to hydroclimate (Ramananantoandro et al. 2016). Lastly, MnD and MxD were related to hydroclimate probably by responding through lagged changes in wood anatomy, specifically tracheid lumen (Camarero et al. 2014; Pacheco et al. 2020). Those lagged responses of wood density to hydroclimate are also relevant patterns which require a better understanding through xylogenesis monitoring.

Conclusions

The minimum wood density of *P. lumholtzii* is a relevant proxy of water availability and drought stress during the early growing season. Both minimum (MnD) and maximum (MxD) wood density provided valuable retrospective information on hydroclimate variation at seasonal resolution. MnD negatively responded to water balance from prior winter to early summer, whereas MxD positively responded to the water balance from winter to spring but negatively to the July water balance. The relationships between seasonal water availability and wood density confirm that *P. lumholtzii* will be more responsive to drought conditions than *P. durangensis*. Changes in wood density and carbon fixation as woody biomass could cascade on modifications of forest productivity and composition.

Author contributions statement MPG and JJC planned and designed the research. MPG was responsible for data collection and conducted fieldwork; AH carried out the laboratory analyses; AH and JJC analyzed the data; MPG led the manuscript with contributions from all authors. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability All data generated or analyzed during this study will be made available upon request.

Code availability We used freeware and open source software.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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