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**High responsiveness of wood anatomy to water availability and
drought near the equatorial rear-edge of Douglas fir**

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Abstract

Wood anatomy is a more precise and informative measure of hydraulic responses to drought than radial growth in trees. Populations located near the equatorial range edge of distribution (rear edge) constitute monitors of responses to hydroclimate. However, their wood anatomy is understudied. We measured tracheid lumen diameter (LD) and cell-wall thickness (CWT) in a rear-edge Douglas fir (*Pseudotsuga menziesii*) population. We also evaluated the formation of intra-annual density fluctuations (IADFs), characterized by earlywood tracheids with narrow lumen. We expected that earlywood (EW) LD, would be particularly sensitive to hydroclimate variability. We found that EW LD was directly related to precipitation during the prior late winter and current spring. Wet conditions were associated to wider EW tracheids and improved growth. These correlations peaked when considering cumulative precipitation from January to May. Earlywood IADFs were formed in response to dry March-April conditions suggesting that dry spring conditions constrained tracheid expansion. The described associations in a rear-edge Douglas fir population confirm a high responsiveness of wood anatomy to drought. We conclude that earlywood lumen diameter is a valuable proxy for hydroclimate reconstruction in Douglas fir.

Key words: drought, intra-annual density fluctuations, lumen diameter, Mexico, *Pseudotsuga menziesii*, wood anatomy.

53 **Introduction**

54 Tree populations acclimate, migrate or become extinct in response to climate changes
55 (Aitken et al. 2008). In drought-prone regions in the northern Hemisphere, tree
56 populations forming the southernmost species distribution limits (rear-edge populations)
57 are expected to show more reduced growth rates than core populations in response to
58 warmer and drier conditions (Loehle 1998). In fact, some rear-edge populations have
59 already displayed long-term radial growth reductions, and high mortality rates in
60 response to drought (Camarero et al. 2015a, 2015b), thus supporting the hypothesized
61 sensitivity of rear-edge forests to water scarcity.

62 Patterns in radial growth can be used as a surrogate measure of tree resilience in
63 response to drought (Gazol et al. 2018). Dendrochronological studies on the equatorial
64 range edge of tree populations (rear edge) have demonstrated drought stress as one of
65 the major growth constraints in those marginal forests (Camarero et al. 2013). However,
66 a more mechanistic view of how drought constrains forest productivity should be based
67 on wood anatomy, which reflects the effects of water shortage on tree functioning
68 because the size of xylem conduits determines hydraulic conductivity and growth (Fonti
69 et al. 2010). Nevertheless, few studies have assessed how wood anatomy, which is the
70 product of xylem dynamics (Vaganov et al. 2006), responds to hydroclimate in
71 American rear-edge populations. In fact most studies on quantitative wood anatomy and
72 xylogenesis have been developed in Eurasian forests (Cuny et al. 2015), whereas many
73 American regions are largely understudied despite they are major centers of diversity of
74 important tree species as pines (Millar 1998). Rear-edge populations are suitable sites to
75 explore climate sensitivity of trees and to analyze wood anatomical proxies suitable for
76 hydroclimate reconstruction (Pellizzari et al. 2016).

Wood-anatomy analyses have detected rapid responses of conduit diameter to seasonal changes in water availability (von Wilpert 1991; Pacheco et al. 2015). In conifers, dry conditions usually lead to the formation of tracheids with smaller lumen and thinner cell walls (Dünisch and Bauch 1994; Abe et al. 2003; Eilmann et al. 2011). However, the responsiveness of transversal lumen diameter and cell-wall thickness to hydroclimate and drought has not been quantified in rear-edge, Douglas-fir (*Pseudotsuga menziesii*) populations. The ample distribution range of Douglas fir along western North America suggests that this species may display large growth plasticity in response to hydroclimate variability. In addition, this study is of regional and global interest since this conifer has been widely planted, and it is a major commercial timber species in America and Europe (Herman and Lavender 1999; Sedjo 2017).

Several studies have assessed the radial-growth responses of Douglas fir to hydroclimate showing that wood formation is constrained by water shortage during spring and summer in natural (Zhang and Hebda 2004; Littell et al. 2008; Griesbauer and Green 2010a, 2010b; Restaino et al. 2016) and planted stands (Bower et al. 2005; Sargent et al. 2014). Quantitative analyses of wood anatomy at the species rear-edge could allow forecasting how projected climate warming will affect Douglas-fir radial growth in its core distribution area. Those analyses would benefit from using rapid assessment techniques of anatomical features as intra-annual density fluctuations (IADFs), which reflect seasonal responses of the xylem to hydroclimate (Vieira et al. 2010; De Micco et al. 2016). In Douglas fir, IADFs are potential hydroclimate proxies (Acosta-Hernández et al. 2018).

In this study, we explore the sensitivity of wood anatomical proxies to climate and drought variability to assess their suitability for hydroclimate reconstruction in a Douglas-fir rear-edge population. First, we provide an assessment of the responses of

lumen diameter and cell-wall thickness to year-to-year hydroclimate variability. Second, we evaluate how these variables respond to intra-annual changes in precipitation, temperature and drought. Third, we introduce a novel method to detect earlywood IADFs using lumen diameter data. We focused on the earlywood because: (i) it accounts for most hydraulic conductivity within the ring, and (ii) it contains IADFs formed by bands of latewood-like tracheids, i.e. cells with small lumen and thick walls (De Micco et al. 2016). We hypothesized that seasonally-derived wood anatomical variables, and particularly earlywood tracheid lumen diameter, are mainly controlled by water availability.

Materials and methods

Study area

Most rear-edge Douglas-fir populations are fragmented and restricted to high-elevation, wet sites subjected to seasonal drought (González-Elizondo et al. 2012). This is the case of the sampled forest (“Las Cebollas”), which is situated in the Sierra Madre Occidental, Durango, northern Mexico. The study site is located at 23° 35’ N and 105° 23’ W at an elevation of 2840 m a.s.l. The nearby climatic station of El Salto (23° 48’ N, 105° 21’ W, 2543 m, period 1946-2016) was used to describe the climate conditions of the site. The study area presents a cool-temperate climate with mean annual temperature of 11.5 °C and annual precipitation of 1100 mm (Supplementary Material, Fig. S1a). The wet and dry seasons last from June to September and from October to May, respectively. Early spring (April), which corresponds to the beginning of the growing season, is the driest period of the year. Trend analyses indicate that climate is warming in the study area, whereas precipitation shows no long-term trend but a high year-to-year variability (Supplementary Material, Fig. S1b).

Tree species

Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a very productive species subjected to ample climatic (range of mean annual temperature from -5° to 22 °C, range of mean annual precipitation from 350 to ca. 3000 mm) and ecological gradients along its natural range of distribution in west North America, from north British Columbia (Canada) to Mexican mountains (Thompson et al. 1999).

Field sampling

We used a sub-set of five trees among those previously studied by Acosta-Hernández et al. (2018). These five trees did not produce reaction wood and showed the highest correlation values with the site mean chronology considering the 1990-2016 period. The Pearson correlation of the selected trees ranged between 0.77 and 0.88, whilst the mean correlation of all measured trees was 0.71.

For each sampled tree three cores were taken per tree at 1.3 m using a 5-mm Pressler increment borer. Two of them were mounted, and sanded to fine grit, measured and averaged to build a site mean tree-ring width (TRW) series chronology, whereas the third core was used for wood-anatomy analyses and it was not sanded. The average diameter at breast height (1.3 m) and height of the whole set of trees were 44.7 cm and 22.1 m, and the mean age was 68 years (Acosta-Hernández et al. 2018). The diameter, height and age variation within the five studied trees were 43.0–47.1 cm, 21.0–24.0 m, and 65–70 years, respectively.

We used standard dendrochronological methods (Fritts 1976) to obtain TRW measurements. Cores were visually cross-dated following the Yamaguchi (1991) method, and tree-ring widths were measured at 0.01 mm resolution using the LINTAB-

TSAP system (F. Rinn, Heidelberg, Germany). The visual cross-dating was checked using the COFECHA program (Holmes 1983).

Wood anatomical measurements

The cores selected for wood anatomical analyses were sectioned using a sledge microtome (Anglia Scientific AS 2000, UK). Thin sections (10-20 μm thick, 4-5 cm long) containing several rings were mounted on glass slides, stained with safranin (0.5% in distilled water) and fixed with Eukitt®. Images of sections (see an example in Supplementary Material, Fig. S2) were first taken at 40–100x magnification with a digital camera mounted on a light microscope (Olympus BH2), and then stitched with the PTGui software (New House B.V., The Netherlands). It must be noted that differences in section thickness and magnification could impact wood-anatomical measurements (Prendin et al. 2017).

We studied the rings formed between 1980 and 2016, which corresponded to mature wood of the trunk sapwood. We measured the lumen diameter (LD) and the tangential double cell-wall thickness (CWT) along the radial direction in five radial lines of tracheids randomly selected in each tree ring using the ImageJ software (Schneider et al. 2012). These two anatomical variables reflect xylem dynamics in conifers (Cuny et al. 2014). We also calculated the LD/CWT ratio to define the latewood (LW) when $\text{LD/CWT} < 2$ according to the Mork index (Denne 1989). To compare patterns of tracheid dimensions (LD, CWT) between rings and years, the number of cells was standardized by using the tracheidogram method (Vaganov et al. 2006) with the 'tgram' package (DeSoto et al. 2011). Following Pacheco et al. (2015) each ring was divided in ten radial sectors or deciles of equal width along the tangential direction with the first and last deciles corresponding to the early earlywood and the late

latewood, respectively (see Supplementary Material, Fig. S3). We also calculated average and standardized values of LD, CWT and LD/CWT for each ring ($n = 190$ rings) and year ($n = 37$ years) following Deslauriers et al. (2003). The mean values of LD and CWT were also separately computed for the earlywood (EW) and the latewood (LW).

Detection of intra-annual density fluctuations

To detect IADFs, we calculated standardized mean tracheidograms for each year using LD data. We considered ten sectors to quantify the LD variability within each ring as explained before. Then, we applied a method to remove the (linear) trend and low-frequency variation from the LD data. The degree of smoothing for lower frequency variation (seasonal component) was selected using an additive decomposition technique. We applied a Seasonal-Trend Decomposition Procedure based on loess (STL) smoothing to analyze the trend and changes in LD over the 1980-2016 period. The loess fit at a particular x value of the LD series is obtained using weighted least squares to fit a polynomial of degree λ to the n_α observations nearest x , where α is the smoothing parameter (Cleveland et al. 1988). STL is a filtering procedure for decomposing a time-series into different components (trend, seasonal and remainder components) by applying loess smoothing (Cleveland et al. 1988, 1990). A time series of LD was regarded as composed of several components: $Y_t = f(S_t, T_t, R_t)$ where, Y_t = raw LD data at period t , S_t = seasonal component at period t , T_t = trend component at period t , and R_t = remainder (error) component at period t . This decomposition technique was used to distinguish the aforementioned components in the LD data. Then, we calculated a random component as $R_t = Y_t - T_t - S_t$, which corresponds to standardized LD residuals. These residuals followed normality. We calculated the lowermost (lower

than the 5% lowest values) values of the LD residuals. These residuals are LD departures from the seasonal mean, and they corresponded to earlywood IADFs formed by bands of tracheids with very narrow lumen.

Statistical procedures

ANOVA with multiple pairwise Tukey's tests were used to compare LD values between years. We removed the long-term trends of wood-anatomy variables by detrending the raw series based on fitting negative linear or exponential functions and then dividing the observed by fitted values to obtain standardized values. Then, to remove their first-order temporal autocorrelation we fitted autoregressive models and the pre-whitened indices were averaged using biweight robust means. In this way we obtained mean residual series or chronologies of LD and CWT for the entire ring and also separately for the EW and LW. A similar procedure was carried out with TRW data to obtain ring-width indices. These analyses were done using the ARSTAN program (Cook and Krusic 2005).

Since precipitation data did not follow a normal distribution (Supplementary Material, Fig. S1a) we used Spearman correlation coefficients to relate monthly and seasonal climate data (mean temperature, total precipitation) from the "El Salto" station with indexed LD and CWT values of the EW and LW. Based on a previous dendrochronological study in this tree population (Acosta-Hernández et al. 2018), we considered the temporal window from previous up to current September for the correlation analyses.

We also correlated climate data with intra-annual LD and CWT values to detect climate-anatomy signals at short temporal scales. Then, we calculated correlations between cumulative monthly precipitation data of the growth year (from January to

September) with the mean LD of each decile. Finally, to assess drought signals in the wood anatomical traits, we correlated the series of earlywood LD, latewood CWT and the annual LD/CWT ratio with the Standardized Precipitation Evapotranspiration Index (SPEI), a multi-scalar drought index with positive and negative values indicating wet and dry conditions, respectively (Vicente-Serrano et al. 2010). We considered again the months of the growth year (January to September), and used 1- to 21-month long SPEI scales (i.e. corresponding to droughts with cumulative water deficits for the past 1 to 21 months). The SPEI was calculated using the SPEI v1.7 library (Begueria et al. 2014) based on climate data from the “El Salto” station. All statistical analyses were done in the R statistical environment (R Development Core Team 2017).

Results

Relationships between wood anatomy and radial growth

The mean ($\pm$ SE) lumen diameter (LD) was $16.34 \pm 0.12 \mu\text{m}$, and the mean cell-wall thickness (CWT) was $7.42 \pm 0.05 \mu\text{m}$ (Figs. 1a and 1b). Considering only EW tracheids, their mean LD and CWT were $23.42 \pm 1.18 \mu\text{m}$ and $6.32 \pm 0.62 \mu\text{m}$, respectively, whereas in the case of LW tracheids their mean LD and CWT were $9.26 \pm 0.80 \mu\text{m}$ and $8.52 \pm 0.28 \mu\text{m}$, respectively (Fig. 1a). The mean TRW of the five selected trees was $1.35 \pm 0.37 \text{ mm}$ (the mean for all trees was $1.27 \pm 0.36 \text{ mm}$; Fig. 1c).

Several years corresponded to high LD values and growth rates such as 1992, 1997, and 2010 (see Supplementary Material, Fig. S4), whereas low LD and growth values were observed in 1999, 2006 and 2011 (Figs. 1a and 1c). Indeed, LD and tree-ring width were significantly and positively related (data were previous log-transformed to achieve normality, $r = 0.67$, $r_s = 0.68$, $P < 0.001$ in both cases; Fig. 2). This association was also observed with residual TRW indices ($r = 0.65$), confirming that it

was not due to first-order autocorrelation in TRW data, since raw and indexed TRW data were tightly associated ($r = 0.82$, $P < 0.001$; Fig. 1c).

The LD reached maximum values in 1997 (31.11 μm and 11.20 μm in the case of EW and LW, respectively), which was a year characterized by a very high growth rate (1.7 mm). The high LD values in EW and LW tracheids of the year 1997 was in agreement with the correlation between LD EW and LD LW, being this relationship similar to that observed between CWT EW and CWT LD (Table 1).

Relationships between climate, drought and wood anatomy

In the case of the EW, CWT decreased with warm May conditions (Fig. 3a), and LD increased in response to high previous winter (January) and current spring (March-April, spring) precipitation (Fig. 3b). Warm current September conditions and wet conditions in the previous autumn and winter were associated with high LD values in the LW, and cool prior-October and wet March and May conditions were related to thick CWT (Fig. 3c). In addition, wet and warm conditions in the prior winter also favored the formation of tracheids with wide lumen (large LD) and thick walls (high CWT) (Fig. 3d). These findings, were also observed when considering the whole tree-ring. Again, significant and positive associations between LD and previous autumn-winter and current spring precipitation were observed for the whole ring (Supplementary Material, Fig. S5). Overall, we found strong links between LD and precipitation. In fact, the cumulative precipitation from January to May was significantly associated to LD (Fig. 4).

Regarding the correlation analyses between cumulative monthly precipitation and LD decile data we found a maximum correlation value ($r_s = 0.59$ - 0.61 , $P < 0.0001$)

for the cumulated precipitation from January to May and the LD value of the third and fourth deciles corresponding to tracheids formed in the earlywood (Fig. 5).

Lastly, the EW LD responded positively to high SPEI values from January to June, mainly at 4- to 11-month long scales (the correlation peaked in March-April considering 8- to 9-month SPEI scales), but no significant correlations were found between LW CWT and the SPEI (Fig. 6).

Earlywood intra-annual density fluctuations

We could detect earlywood IADFs using our automatic method based on the analysis of LD data. The IADFs were characterized by several rows (usually from 3 to 5) of tracheids with narrow lumen (see Fig. S2). IADFs were very noticeable in 1998, 2003 and 2007, when the residuals of LD reached minimum values (Fig. 7), but they were also detected in 1995, 1996, 1999, 2000, 2002, 2006, and 2008. Those years were characterized by dry spring conditions. For instance, March-to-April precipitation of years with evident IADFs (mean $\pm$ SE = 4 ± 2 mm) was 9% of the mean for years without IADF (39 ± 11 mm).

Discussion

We found support for our hypothesis that wet conditions favored the formation of xylem conduits with wider lumen and, therefore, increased the theoretical hydraulic conductivity. High precipitation during the prior late winter and early spring promoted the formation of earlywood tracheids with wide transversal diameter in the study rear-edge Douglas fir population. Specifically, the correlations peaked when considering cumulative precipitation from January to May and the lumen diameter (LD) of tracheids located in the second decile, i.e. corresponding to the early earlywood. When

considering the SPEI drought index the correlation with LD peaked from January to June, and corresponded to water balance accumulated since the prior October. Lastly, the method used (STL) allowed detecting earlywood intra-annual density fluctuations (IADFs), characterized by several rows of tracheids with narrow lumen, which were formed in response to dry March-April conditions. This method offers an efficient and reliable method to detect anomalies in LD, including IADFs. It could be used to detect changes in LD or CWT in response to other stress factors including droughts, frosts, or insect defoliations.

Overall, our findings support that precipitation from winter to spring affects the LD and, therefore, influences the potential hydraulic conductivity (Fonti et al. 2010). We found a tight relationship between LD, a proxy of hydraulic conductivity, and radial growth. Such relationship agrees with a previous study on a high-elevation pine species (Camarero et al. 1998). Consequently, drought during the growing season decreases tracheid expansion, hydraulic conductivity and radial growth (Eilmann et al. 2009; Bryukhanova and Fonti 2013). Such decrease in lumen diameter would result in denser wood with higher strength (Zobel and Van Buijtenen 1989). The analyses of climate-LD associations are consistent with the finding that earlywood IADFs were formed in response to dry spring conditions (Acosta-Hernández et al. 2018). We show that automatic methods based on LD data are promising tools for developing and quantifying new hydroclimate seasonal proxies as IADFs in Douglas fir as in other conifers subjected to seasonal drought (De Micco et al. 2016).

Interestingly, cool-wet conditions in the prior autumn and winter also enhanced the LW LD, which may be an indirect consequence of the positive effects on EW LD. Both EW LD and LW LD were positively correlated suggesting that the formation of wider tracheids in the early growing season, when conductivity probably peaks,

determines to some degree the formation of wider tracheids in the late growing season when conditions become wetter due to the summer monsoon (Adams and Comrie 1997). In fact, the latewood production in SW North America forests is a proxy of summer monsoon precipitation (Griffin et al. 2013), but we should investigate how this climate signal depends on wood-anatomical features such as EW LD in the future. Xylogenesis studies in similar rear-edge tree populations would allow determining when EW and LW are formed, and how wood-anatomical features (LD, CWT, LD/CWT ratio) respond to short-term climate variability.

Regarding the CWT, we found that it increased in response to wet spring and prior-winter conditions in the EW and LW, respectively. In contrast with LD, CWT did not show significant correlations with the SPEI drought index. Unexpectedly, we did not detect significant associations between LW CWT and summer climate conditions. This could indicate that LW CWT mainly depends on LW LD, and indirectly on EW LD. In general, our results are in agreement with previous studies on conifer species, in which CWT was found to decrease in both earlywood and latewood under warmer and drier conditions (Eilmann et al. 2009; Fonti et al. 2013; Martín-Benito et al. 2013; Heres et al. 2014).

The observed relationships between climate, lumen diameter and cell-wall thickness suggest that Douglas-fir wood has evolved to provide hydraulic safety. This interpretation is supported by the positive association between hydraulic capacitance and latewood proportion observed in this species (Domec and Gartner 2002). Therefore, the latewood may act as water storage tissue, whenever low pressures and related xylem embolism do not occur. The strong responsiveness of EW LD to water availability agrees with Douglas fir ecophysiological strategies since it is considered within isohydric species as it avoids drought stress by rapidly reducing stomatal conductance

to limit water loss through transpiration but maintaining a constant leaf water potential (Bauerle et al. 1999). In addition, water deficit during the growing season reduces Douglas-fir photosynthesis rates (Lassoie and Salo 1981), which may contribute to reduced EW formation.

The responses of the two Douglas-fir wood-anatomical features to hydroclimate variability were significant. These responses could be mediated by low soil moisture values at the study site, which would reduce water availability to trees given the high evapotranspiration rates of Douglas fir (Andrews et al. 2012). Nevertheless, the soil water-holding capacity can only partially explain the responsiveness of Douglas-fir xylem to drought, even if some trees are able to access deep water sources (Andrews et al. 2012).

Our results agree with previous dendrochronological analyses in Douglas-fir Mexican populations, which aimed to reconstruct hydroclimate variability and found a tight relationship between EW formation and the rainfall accumulated from the prior late winter to the early spring (Villanueva-Díaz et al. 2009). However, these authors could not achieve robust reconstructions of summer precipitation, which could be more linked to LW production. Our findings indicate that their interpretation may be correct since we did not find significant associations between LW anatomical variables and summer precipitation. However, our study also explains how the enhancement of EW production under wet early growing-season conditions may be due to the production of wider and more numerous EW tracheids. This could be extended to other conifers inhabiting drought-prone areas as wet and cool winter-to-spring conditions have been found to promote growth of Mexican pine species near the study area (González-Cásares et al. 2017).

Douglas fir shows natural genetic adaptation to local climate and drought (Bansal et al. 2015). Accordingly, Douglas-fir populations best adapted to cope with forecasted drought conditions would be those from regions with relatively cool winters and arid summers. However, the frequency of extreme climate events such as severe droughts can increase in the forthcoming decades. Such drying trends could negatively impact Douglas-fir growth and productivity. This loss in productivity was observed during the 2003 drought and heat when dieback and mortality episodes affected European Douglas-fir plantations (Sergent et al. 2014). Reductions in lumen diameter and radial growth could be used as early-warning indicators of forest productivity loss in response to dry spells. We also show that the xylem responsiveness to hydroclimate is high in rear-edge tree populations when it is properly analyzed and quantified. Although we found a pronounced xylem sensitivity to early growing-season precipitation in a rear-edge Douglas fir population, we consider that other forests located near the “core” of the distribution range but subjected to seasonal droughts or located in xeric sites (e.g., in steep slopes with shallow soils) could show similar responses (Griesbauer and Green 2010a). Our results could be also used to suggest strategies for forest management as climate changes become more apparent. Understanding the influences of water availability on conduit size (lumen and cell-wall dimensions) can provide useful proxies to forecast physiological adjustments to future environmental conditions.

To conclude, the cumulative precipitation from the prior winter up to spring influences the EW lumen diameter, a proxy of the theoretical hydraulic conductivity (Hacke et al. 2015), and also affects radial growth. Earlywood IADFs reflect dry spring conditions. Winter to spring wet conditions enhance the formation of wider tracheids which provide more hydraulic conductivity and allow increasing growth. Since most

Douglas-fir forests are water-limited (Restaino et al. 2016), our wood-anatomical investigations on a rear-edge Douglas-fir population provide relevant information to project forest productivity in response to a warmer and drier climate at the core of the species distribution area.

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Table

Table 1. Spearman correlations calculated among the mean series of lumen diameter and cell-wall thickness measured in the earlywood (EW) and latewood (LW) considering the period 1980-2016. Significance values are shown between parentheses.

Variable	Wood type	Lumen diameter		Cell-wall thickness
		EW	LW	EW
Lumen diameter	LW	0.303 (0.068)		
Cell-wall thickness	EW	0.201 (0.231)	0.616 (0.001)	
	LW	0.151 (0.368)	0.061 (0.717)	0.302 (0.068)

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Figure captions

Figure 1. Mean annual values of (a) lumen diameter (LD) and (b) cell-wall thickness (CWT) separately presented for earlywood and latewood tracheids, and (c) mean series of tree-ring width (line with symbols) and ring-width indices (black line without symbols). The error bars are SE. The grey lines in the lowermost plot show the individual series of ring-width indices for the trees selected for wood-anatomical analyses.

Figure 2. Relationship observed between the mean annual values of tracheid lumen diameter and tree-ring width. Correlations and significance levels are presented either for log-transformed (Pearson r) or raw data (Spearman r_s). The linear regression is presented with 95% confidence intervals (dashed lines) and prediction intervals (grey lines). The inset shows the raw data relationship.

Figure 3. Relationship between climate and wood anatomical traits (lumen diameter and cell-wall thickness). Spearman correlation coefficients and significance levels are shown considering the earlywood (EW) and latewood (LW). Dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively. Monthly and seasonal climate data are mean temperatures (a, c) and total precipitation (b, d) and go from the previous-year (months abbreviated by lowercase letters) up to current-year September (months abbreviated by uppercase letters).

Figure 4. Positive association found between the summed precipitation from January to May and tracheid lumen diameter. The Spearman correlation value (r_s) is presented with

its significance levels (P) considering all data or removing the 1997 outlier (big symbol). The linear regression is presented with 95% confidence intervals (dashed lines) and prediction intervals (grey lines).

Figure 5. Spearman correlations calculated between cumulative monthly precipitation and tracheid lumen diameter. The lumen diameter was calculated as mean values for the radial deciles comprising the tree ring (x axis). The grey scale indicates the cumulative precipitation for each month (e.g. the July bar is the precipitation accumulated from January up to July). The dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively.

Figure 6. Drought-anatomy associations assessed in Douglas fir for the lumen diameter of earlywood (EW) tracheids (a) and the cell-wall thickness of latewood (LW) tracheids (b). Drought was quantified using the SPEI drought index calculated at 1- to 20-month-long scales (x axes) from January to September of the growth year (y axes). Correlations (scale color and legend) above 0.38 and 0.46 are significant at the 0.05 and 0.01 levels, respectively.

Figure 7. Results of the analysis of intra-annual density fluctuations (IADFs) based on lumen diameter (LD) data and following the tracheidogram approach. (a) Normalized values of lumen diameter values (black line) with trend (blue line) and seasonal (red line) components. (b) Random component of lumen diameter extracted after removing the trend and seasonal component and lowermost values (residuals lower than the 5% distribution) corresponding to earlywood IADFs (red dots).

Figures

Figure 1.

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