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Minimum wood density is a robust proxy of spring water availability and
drought stress in continental Mediterranean climate

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Abstract

Aim

Climate warming and associated aridification have been forecasted for the Mediterranean Basin, which is considered a climate-change hot-spot. Such drying trends could affect the performance and growth of conifers in these drought-prone areas. We evaluate if radial growth and wood density constitute potential proxies of precipitation and drought in a Mediterranean conifer.

Location *Juniperus thurifera* Iberian forests in northern and eastern Spain.

Methods

We sampled ten stands encompassing the species' distribution area. We related several annually resolved tree-ring variables (earlywood and latewood width, maximum and minimum wood density) to climatic factors (temperature, precipitation, drought index) for the period 1951–2000. We analyzed the spatial and temporal patterns of those associations.

Results Minimum wood density presented the strongest response to climate of all analyzed tree-ring variables. Higher values of the minimum wood density were related to drier spring conditions, particularly in the most xeric sites, confirming that a drought-induced reduction in the radial expansion of tracheids increases earlywood density.

Main conclusions Minimum wood density is a biogeographically meaningful proxy of spring water availability and drought stress for Mediterranean conifers.

Key words: dendroclimatology; dendroecology; *Juniperus thurifera*; Mediterranean climate; Spain; wood density.

Abbreviations:

EW, earlywood width;

LW, latewood width;

Dmin, minimum wood density;

DMax, maximum wood density;

Prec, total precipitation;

Tmin, monthly mean minimum temperatures;

Tmax, monthly mean maximum temperatures.

Introduction

The several functions performed by wood in trees (mechanical support, water and carbon storage, water transport, defense) seem to be reflected by wood density, which has emerged as a variable integrating these diverse and often conflicting functions (Chave *et al.*, 2009). In general, dense wood is resistant to breakage, implosion and decay (Niklas, 1992). The current paradigm holds that high wood density provides greater strength and resistance to implosion and decay but entails higher construction costs and is linked with a lower growth rate (Muller-Landau, 2004). A reduction in conduit diameter, usually linked to a denser wood (but see Poorter *et al.*, 2010), provides a higher resistance to water flow but reduces xylem vulnerability, especially with respect to freezing-induced cavitation, thus leading to a functional tradeoff (Baas *et al.*, 2004).

In conifers, tracheids must provide mechanical resistance and hydraulic conductivity (Larson, 1994). In such species wood density is also closely related to the ratio of cell wall thickness to transversal lumen diameter or thickness-span ratio (Yasue *et al.*, 2000). This ratio is considered a good surrogate of xylem resistance against embolism (Hacke *et al.*, 2001). A less dense wood with lower mechanical strength may increase hydraulic efficiency if tracheid lumen enlarges (lower thickness-span ratio), and this would also reduce formation costs per wood volume. Following this line of reasoning, conifers would tend to produce a denser wood in response to dry conditions. These apparent trade-offs have been empirically evidenced in species of both Pinaceae and Cupressaceae whose wood showed parallel trends of thickness-span ratio, wood density and embolism resistance (Pittermann *et al.*, 2006). However, counterintuitive results may also occur and larger tracheids have been reported in drier provenances as an adaptation to maximize water uptake (Martín *et al.*, 2010). Thus, such presumed tradeoffs in tree function may reflect correlated evolution on different sets of co-varying traits and caution may be taken

when interpreting them (Larjavaara & Muller-Landau, 2010).

Conifer latewood tracheids laid down during summer and autumn are smaller, denser, darker and mechanically stronger than earlywood tracheids (Larson, 1994). Earlywood may represent from 50 up to 95% of the ring width and its transition to latewood is triggered by a decrease in available soil moisture and a reduction in auxin production (Larson, 1994). Dendroclimatological studies have normally used maximum wood density of conifers as a proxy of summer temperature variability in cold areas such as boreal or subalpine forests (Wang *et al.*, 2002; Wimmer & Grabner, 2000). Maximum latewood density is highly correlated with cell wall thickness whose highest value is recorded in the middle of the latewood zone (Yasue *et al.*, 2000). After the cessation of radial expansion of tracheids, secondary cell wall formation and lignification persists for several weeks in latewood (Wodzicki, 1971; Gindl *et al.*, 2000), explaining the positive influence of summer temperatures on the maximum latewood density. For instance, low temperatures in the late growing season induce the formation of “light rings” in boreal conifers, i.e. tree rings with low density latewood (Filion *et al.*, 1986).

Each stage of xylem differentiation is affected by different environmental constraints (Vaganov *et al.*, 2006). Hence, it can be hypothesized that several wood-density measures (e.g., maximum vs. minimum density) should respond to different climatic factors. In contrast to the strong positive relationship observed between maximum wood density and summer temperatures (Briffa *et al.*, 2004), the effects of precipitation on wood density show a strong variability among species presenting either negative responses to summer precipitation (Yasue *et al.*, 2000; Büntgen *et al.*, 2010) or negative and positive responses to late previous-winter and summer precipitations, respectively (Gagen *et al.*, 2006; Büntgen *et al.*, 2010). In spite of the abundant literature on the maximum density responses to climate, the climatic signal of minimum density remains largely unexplored in spite of

promising results (Cleaveland, 1986).

Soil water content modulates lumen size by influencing turgour pressure of differentiating tracheids (von Wilpert, 1991). An increase in water deficit during the early growing season leads to a reduction in lumen size (Bouriaud *et al.*, 2005; Olano *et al.*, 2012). This theoretical background leads us to expect the formation of a denser earlywood formed by narrow tracheids with thick walls in response to dry spring conditions. Accordingly, we hypothesize that minimum (earlywood) density would be a potential ecologically valuable proxy of rainfall variability in continental Mediterranean climates where both growth and carbon gain peak in spring and are constrained by winter coldness and summer drought (Camarero *et al.*, 2010; Gimeno *et al.*, 2012). The search of robust proxies to provide a long-term perspective on growth responses to climate is crucial for understanding how tree species tolerate different levels of stress (Fonti & García-González, 2008). This exploration is very relevant in the Mediterranean Basin which is considered a major climate-change hot-spot where both warming and aridification trends have been observed (Giorgi, 2006). We test these ideas by relating several annually resolved tree-ring variables (earlywood and latewood widths, maximum and minimum wood densities) to climatic factors (temperature, precipitation, drought index) during the second half of the 20th century across a network of *Juniperus thurifera* L. Iberian forests encompassing diverse climatic and biogeographical characteristics.

Materials and Methods

Study species

Juniperus thurifera L. is a tree endemic to the western Mediterranean Basin with most extant populations being found in continental and dry areas of Spain and Morocco (Gauquelin *et al.*, 1999). In this species radial growth is driven by winter rainfall, spring

temperature, and summer water stress (Bertaudière *et al.*, 1999; Rozas *et al.*, 2009; DeSoto *et al.*, 2012). Xylogenesis initiates from April to May and extends until October-November, with a summer arrest in semiarid locations (Camarero *et al.*, 2010). Tracheid anatomy is controlled by rainfall and temperature, which show multiple shifts in a variable way during the period of formation (Olano *et al.*, 2012).

Study area

We sampled 10 sites across the Iberian distribution area of Spanish juniper. Two sites (LA; LU) were located in the Northwestern fringe of the Spanish Central Plateau or “Meseta” (42° 50’-42° 52’ N, 4° 51’-5° 51’ W, 1235 m a.s.l.) in areas characterized by wet and cool winter (3.0 °C, 330 mm) and spring (8.9° C, 252 mm) conditions (Fig. 1). Five sites are located in Western Meseta (sites AR, SI, CI, CH and BU; latitude 40° 08’-42° 02’ N, longitude 1° 56’-3° 38’ W, mean elevation 1319 m). These sites experience cold winters (mean temperature 3.0 °C) and dry summers (total precipitation 105 mm). Other two sites (VE, VI) were located in Southeastern Spain (38° 48’-40° 09’ N, 1° 25’-2° 31’ W, 1202 m), an area characterized by cold winters (4.0 C°) and hot and dry summers (22.0 °C, 70 mm). Finally, a single site (SE, 41° 46’ N, 0° 32’ W, 530 m) was sampled in the lowland steppes of North East Spain where winters are mild (5.9 °C), summers are dry (65 mm) and hot (23.6 °C) and the wet seasons are spring (107 mm) and particularly fall (160 mm) (Fig. 1). Climate data for the sampling sites were obtained from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola *et al.*, 2000).

Field sampling and density measurements

We sampled from 7 to 20 dominant trees per site (on average 16 trees per site). We measured the diameter at 1.3 m (diameter at breast height, hereafter abbreviated as dbh) of

trees and took wood cores at that height using increment borers. Wood samples were processed (sanded, visually cross-dated and checked for dating accuracy) using standard dendrochronological methods as explained in DeSoto *et al.* (2012). Tree samples were finally selected according to tree age. We analyzed only those samples from 70-100 years old trees (Table 1) since cambial age affects wood density (Franceschini *et al.*, 2013).

One radial X-ray density profile was obtained from each tree using indirect X-ray microdensitometry (Polge, 1966). First, each core was carefully sawn using a double blade saw to obtain 1.5-mm thick and 5-mm wide wood slices. Second, these samples were air dried up to moisture equilibrium and subsequently subjected to X-ray exposure. The resulting X-ray films were scanned at 1000 dpi of resolution with 8 bits per pixel. The digitalized images were processed using WinDENDRO (Regent Instruments Inc., Canada). All densitometric analyses were performed in the Unité Amélioration, Génétique et Physiologie (INRA, Orléans, France).

The last step of the data process used a routine written in R language (R Development Core Team, 2012) to compute the following parameters: earlywood width (hereafter abbreviated as EW); latewood width (abbreviated as LW); minimum density (abbreviated as DMin) and maximum density (abbreviated as DMax) (see Fig. 2). Density profiles were separated into annual rings following Rozenberg *et al.* (2001). Earlywood and latewood were distinguished based on the DMin and DMax values and the total width of each ring (see Mothe *et al.*, 1998; Koubaa *et al.*, 2002). The definitions of earlywood and latewood used here are based on density changes along the tree-ring and do not correspond to the anatomical definitions of earlywood and latewood. For instance, the earlywood based on anatomical data for *Juniperus thurifera* may comprise more than 90% of the whole ring width (Olano *et al.*, 2012), whereas this percentage decreases when densitometric criteria are applied.

Chronology building

Four chronologies of the aforementioned variables were calculated for each site using the ARSTAN program (Cook & Krusic, 2005). First, the individual tree series were detrended by fitting negative exponential or linear functions. Second, cubic smoothing splines with a 50% frequency response of 32 years were applied. Then, the actual values of EW, LW, DMin and DMax were divided by the fitted values to generate dimensionless and standardized indices. To remove autocorrelation each standardized series was prewhitened through autoregressive modelling producing residual series. Finally, the obtained residual indices were averaged on a year-by-year basis using a bi-weight robust mean, which reduces the effects of outliers, producing a site chronology for each variable. Composite mean chronologies for the whole studied Iberian region were built for each variable by averaging the local site chronologies.

To compare and to evaluate the quality of the site chronologies, several descriptive statistics (Fritts, 2001) were calculated for the common interval 1951–2000 from the standard (raw data) chronologies (mean, SD and AC) and also from the residual ones (MSx, EPS, PC1 and SNR). Mean and SD are the mean value and its standard deviation. AC is the first-order autocorrelation, a measure of the year-to-year growth or density similarity. Mean sensitivity (MSx) is a measure of the year-to-year variability in a variable (width or density) of consecutive tree rings. The expressed population signal (EPS) measures the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley *et al.*, 1984). PC1 is the growth variance explained by the first principal component. Finally, the signal-to-noise ratio (SNR) is a measure of the strength of the common high-frequency signal in a given variable of trees from the same site. Lastly, we used Varimax rotated principal component analysis to

define regional groups of neighbouring sites based on their common EW variability, revealed as a good proxy of total tree-ring width, during the period 1951–2000 (see also DeSoto *et al.*, 2012). We also calculated inter-site correlations of the four wood variables and plotted them as a function of distance to assess its spatial autocorrelation.

Analysis of growth and density responses to climate

We analyzed the responses of the four wood variables to climate by calculating Pearson correlation coefficients between site residual chronologies and corresponding monthly climatic variables (Tmin and Tmax, monthly mean minimum and maximum temperatures; Prec, total precipitation) for the period 1951–2000. We used the 0.5°-gridded CRU TS 3.0 data set, which was built using instrumental records from a global network of meteorological stations (Mitchell & Jones, 2005). To represent drought stress and related soil moisture availability we used the Palmer Drought Severity Index (hereafter abbreviated as PDSI) which is calculated using the interpolated fields of monthly precipitation and temperature observations of the CRU data set (van der Schrier *et al.*, 2006). We compared growth and climatic variables considering a 13-month time window encompassing from September before tree-ring growth starts up to September of the year of tree-ring formation. This window was selected based on previous dendroecological and xylogenesis studies on *J. thurifera* (Bertaudière *et al.*, 1999; Rozas *et al.*, 2009; Camarero *et al.*, 2010; Rozas & Olano, 2013). Finally, we related 0.5°-gridded climatic data (May Tmax and June PDSI) with the mean of all DMin site chronology representing the whole studied greater Iberian region. We downloaded the climatic data and calculated the spatial correlations using the Climate Explorer web (<http://climexp.knmi.nl>).

Results

Growth and density patterns within and among sites

On average, *J. thurifera* formed rings with mean ($\pm$ SD) EW and LW values of 0.95 ± 0.65 and 0.43 ± 0.22 mm, and DMin and DMax values of 0.44 ± 0.05 and 0.64 ± 0.07 g cm⁻³, respectively (Table 2). Wood of trees from the most xeric sites (SE, VE and VI) showed the highest DMin values. The variables with the highest AC and MSx mean values were DMax and LW, respectively. The strongest coherency within sites (lowest variability among trees) was found for the DMin (global means: EPS = 0.82, PC1 = 46.7%, SNR = 4.70) and EW (EPS = 0.78, PC1 = 45.9%, SNR = 4.55) series (Table 2).

DMin chronologies were negatively and significantly ($P < 0.05$) correlated to EW and LW series in seven and eight of the study sites, respectively (results not presented). EW and LW chronologies were also positively and significantly related among them in six sites, while in four sites the EW series of the previous year were significantly associated to LW series of the following year.

The highest common variability among site chronologies was observed for DMin (the first principal component accounted for 48.6% of variance) followed by EW (the first principal component accounted for 34.5% of variance) (Fig. 3). Accordingly, the distance among sites explained 24% of the similarity among DMin site chronologies, whereas distance only explained 7%, 5% and 4% of the similarity among Dmax, EW and LW chronologies, respectively (Fig. 4).

Responses of growth and density to climate and drought

EW responded positively to warm and wet springs and dry conditions in the previous winter, whereas LW responded positively to warm conditions in late winter and wet conditions in late spring (Fig. 5). The Dmax climatic signal at the site level was usually not significant and this variable only showed negative responses to previous January

precipitation and late-summer PDSI (Fig. 6). Contrastingly, Dmin showed the highest frequency of significant correlations between wood traits and climatic variables (Fig. 6). May and June were the most influential months of Dmin with a negative relation with May and June Tmax and positive signals of May and June rainfall. Dmin also showed negative responses to PDSI during the growing period. In agreement with the local responses, mean composite chronologies for Dmax and Dmin (Fig. 7) showed strong and negative relationships with winter (December and January) and spring (April to June) accumulated rainfall, respectively.

Local responses of DMin to drought showed a clear spatial pattern across the sampled area with most xeric sites (VE, VI and SE) presenting the most negative responses to June PDSI (Figs. 6 and 8). In a broader geographical context considering the whole studied Iberian region, the response of the composite DMin chronology to June PDSI was geographically focused on the northeastern xeric SE site while the response of DMin to May Tmax spread over most of the Iberian Peninsula and northern Morocco (Fig. 9).

Discussion

Drier conditions in the early growing season are linked to a denser earlywood, *i.e.* higher values of minimum wood density, in *Juniperus thurifera*. This confirms that minimum wood density is a robust proxy of spring water availability in areas subjected to seasonal droughts such as Mediterranean regions. We also show that the link between this proxy and spring water availability is strongest in the driest sites and it is also spatially structured in the Iberian Peninsula during the second half of the 20th century.

An improved water status has been linked to the production of rings with lower mean density (Lundgren, 2004) and wider earlywood tracheids (Olano *et al.*, 2012). The negative response of minimum density to spring water availability agrees with our

knowledge on *J. thurifera* xylogenesis since the maximum rates of tracheid production occur during May and June (Camarero *et al.*, 2010). The minimum wood density along an annual tree ring is usually observed in the first third of the whole ring, i.e. in the early earlywood (Mothe *et al.*, 1998; Vaganov *et al.*, 2009). A dry early growing season is probably linked to the production of narrow earlywood tracheids and a denser earlywood. This result is consistent with the finding of a negative association between minimum wood density and spring precipitation in semiarid sites of the southwestern USA (Cleaveland, 1986) and suggests that this relationship should hold for drought-prone environments. In any case, our results imply that spring drought induces the formation of a more costly earlywood in terms of carbon investment which agrees with the increased tracheid lignin content in drought-stressed Austrian pines (Gindl, 2001).

In fact, a drought-related reduction of the lumen diameter of earlywood tracheids and an increase in earlywood density is supported by experimental evidence. Throughfall exclusion reducing the soil moisture in a Canadian balsam fir forest which lead to the formation of fewer and smaller tracheids, with thicker cell walls, and also to a delayed start of the differentiation process of cambial derivatives (D'Orangeville *et al.*, 2013). In the same way, drought caused the formation of thicker walls of latewood tracheids in Norway spruce (Jyske *et al.*, 2010), consequently increasing the maximum wood density. However, these evidences are not conclusive, since reduced soil water potential during the growing season decreased radial increment of Norway spruce but had a small influence on tracheid dimensions and wood density (Lundgren, 2004). The picture may be even more complex, since in Scots pine larger tracheids with thinner cell walls were found in drought-exposed Scots trees (Eilmann *et al.*, 2011). Anyway, a strong positive signal between June rainfall and lumen size of earlywood tracheids has been confirmed for *Juniperus thurifera* in our study area (Olano *et al.*, 2012).

Earlywood tracheids with narrower lumens produced during dry springs and corresponding to higher minimum wood density are expected to be less conductive and less vulnerable to cavitation than wider tracheids (Hacke *et al.*, 2001). Empirical evidence based on a comparison of Douglas-fir clones has shown that those clones most resistant to drought-related cavitation also presented the highest minimum wood density values (Dalla-Salda *et al.*, 2009). Under mesic conditions, the earlywood transports water more efficiently than the latewood, whereas the latewood presents a higher resistance to xylem embolism than the earlywood under dry conditions (Domec & Gartner, 2002). This could explain why trees with higher percentage of latewood are found under the most arid conditions (Barajas-Morales, 1985).

Width and density variables may host redundant information (Cleaveland, 1986). This was also noted in this study since minimum density and earlywood width were negatively related suggesting that enhanced radial growth leads to the formation of a less dense earlywood. However, this relation may have a mechanistic explanation because an improved hydraulic conductance may enhance growth rates (Ze-Xin *et al.*, 2012) with larger tracheids leading to wider rings. Furthermore, an improved growth during the early growing season usually precedes a greater production of latewood, possibly because an enhanced carbohydrate synthesis during spring is coupled with intense lignification rates and cell wall synthesis of latewood tracheids (Pasho *et al.*, 2011). Analogously, warm summers increased the maximum ring density in boreal conifers but this signal is also affected by carryover effects such as the positive influence of spring temperatures on tree-ring width (Kirdyanov *et al.*, 2007), a response which is also observed in maximum density series of Pyrenean and Alpine high-elevation conifer forests (Büntgen *et al.*, 2010, 2012). Further studies should determine if the observed associations between winter conditions and maximum wood density are a consequence of stored carbohydrates synthesized during

that season, or caused by indirect effects on earlywood growth, taking into account that latewood formation in *J. thurifera* starts in summer (Camarero *et al.*, 2010).

The mentioned diverse wood responses of conifers to climate may be caused by several factors including: (1) climatic, biogeographic or genetic differences between boreal and Mediterranean conifer species or provenances; (2) long-term adaptive responses to dry conditions, or (3) phylogenetic constraints among conifer families. First, maximum density is a robust proxy of summer temperature in boreal (Briffa *et al.*, 2004; Grudd, 2008) and alpine Mediterranean regions (Büntgen *et al.*, 2010). However, this was not the case of *J. thurifera* maximum density which responded to previous fall rainfall whereas tree-ring width did it negatively (Rozas *et al.*, 2009). These signals emphasize the relevance of previous fall-winter conditions in continental Mediterranean climates on subsequent carbon uptake (Gimeno *et al.*, 2012), radial growth (DeSoto *et al.*, 2012) and latewood thickening. On the other hand, latewood width was enhanced by spring precipitation which suggests that the definition of this variable based on densitometry may yield relevant climatic information. Second, our findings indicate that the most xeric sites (e.g., site SE) were the most responsive to precipitation in terms of changes in minimum wood density. This was also observed in Norway spruce populations under drought-prone conditions (Franceschini *et al.*, 2013). Third, phylogenetic constraints do not suffice to explain the diverse wood responses to climate since similar trade-offs between wood anatomy and density appear in species of Pinaceae and Cupressaceae (Hacke *et al.*, 2001). One of the xylem evolutionary adaptations of Cupressaceae conifers to withstand drought and dominate arid areas may have been through changing the number and size of earlywood tracheids (Pittermann *et al.*, 2012), reflected as variations in minimum wood density.

To conclude, we have shown that minimum wood density is a robust proxy of spring water precipitation in Mediterranean areas where maximum wood density does not

portray so much climatic information. Our results indicate that the link between minimum wood density and spring rainfall was geographically consistent during the last half of the past century. Such proxy may yield valuable socio-economic information in drought-prone areas to reconstruct past spring water availability and related agricultural and environmental information such as cereal harvests or water resources. To accomplish this, two objectives must be met first. One, we require a better evaluation of the wood anatomical and growth variables determining earlywood density in Mediterranean conifers. Second, we need longer density chronologies of *J. thurifera* from Mediterranean areas to assess if the link between spring precipitation and minimum wood density is temporally stable. This would allow comparing climate-growth-density links between temperature-limited boreal and water-constrained Mediterranean conifer forests. Tree-ring width, maximum wood density and summer temperature have exhibited divergent trends across northern conifer forests during the late 20th century (Briffa *et al.*, 1998; Franceschini *et al.*, 2012). Several global-change drivers such as nitrogen fertilization (Mäkinen *et al.*, 2002) or rising CO₂ atmospheric concentrations (Kostiainen *et al.*, 2004) could explain these divergent trends. Yet, our findings do also suggest considering precipitation and drought stress as additional divergence factors controlling wood density.

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Biosketches

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Author contributions: JJC led the writing and drafted the manuscript, which was approved by all authors. VR and JMO corrected previous versions of the manuscript. VR and JJC analysed the data. VR and JMO designed the study, conceived the ideas and supervised densitometric measurements. All authors performed field sampling, collected the data and contributed to the discussion.

Tables

Table 1. Geographical, topographical and structural features of the study sites (mean $\pm$ SE). The last column shows the number of trees sampled in each site. Site locations are displayed in Figure 1.

Site (code)	Region	Elevation (m a.s.l.)	Age (years) [§]	Dbh (cm)	No. trees
Peña Lampa (LA)	North West	1187	95 $\pm$ 15	20.7 $\pm$ 3.1	20
Mirantes de Luna (LU)	North West	1284	103 $\pm$ 12	16.8 $\pm$ 2.5	12
Arlanza (AR)	Central Plateau (Meseta)	932	72 $\pm$ 4	27.1 $\pm$ 5.1	20
Buenache (BU)	Central Plateau (Meseta)	1319	84 $\pm$ 8	31.9 $\pm$ 6.5	20
Chaorna (CH)	Central Plateau (Meseta)	1210	93 $\pm$ 15	37.2 $\pm$ 7.2	26
Ciria (CI)	Central Plateau (Meseta)	1157	87 $\pm$ 11	30.7 $\pm$ 4.4	16
Sigueruelo (SI)	Central Plateau (Meseta)	1114	156 $\pm$ 20	50.4 $\pm$ 9.5	7
Santa Engracia (SE)	North East	530	77 $\pm$ 16	18.9 $\pm$ 3.0	10
Veguillas (VE)	South East	1375	126 $\pm$ 18	38.2 $\pm$ 8.1	16
Viveros (VI)	South East	1030	80 $\pm$ 8	26.7 $\pm$ 4.6	13

[§]Age was estimated at 1.3 m based on the maximum number of rings counted in each tree.

Table 2. Comparison of dendrochronological statistics calculated for the standard and residual site chronologies of four wood variables (EW, earlywood width; LW, latewood width; DMin, minimum density; DMax, maximum density) considering the common period 1951–2000. See sites' codes in Table 1.

Variable	Site	Standard chronologies		Residual chronologies				
		Mean $\pm$ SD (mm or g cm ⁻³)	AC	MS _x	EPS	PC1 (%)	SNR	
EW	LA	0.71 $\pm$ 0.37	0.51	0.40	0.78	52.0	4.02	
	LU	0.37 $\pm$ 0.26	0.61	0.32	0.81	45.7	4.21	
	AR	1.09 $\pm$ 0.83	0.45	0.44	0.64	41.0	3.84	
	BU	1.07 $\pm$ 0.80	0.42	0.41	0.81	45.8	4.34	
	CH	0.96 $\pm$ 0.57	0.56	0.32	0.84	50.0	4.87	
	CI	0.86 $\pm$ 0.25	0.66	0.30	0.87	55.3	5.07	
	SI	1.28 $\pm$ 1.10	0.39	0.48	0.85	53.7	5.00	
	SE	1.05 $\pm$ 0.90	0.34	0.49	0.79	39.8	4.85	
	VE	0.88 $\pm$ 0.40	0.61	0.41	0.79	39.4	4.59	
	VI	1.18 $\pm$ 1.04	0.30	0.42	0.66	36.7	4.69	
LW	LA	0.35 $\pm$ 0.20	0.16	0.45	0.46	38.8	0.65	
	LU	0.24 $\pm$ 0.14	0.51	0.30	0.70	42.6	2.33	
	AR	0.41 $\pm$ 0.18	0.10	0.55	0.31	28.6	0.67	
	BU	0.48 $\pm$ 0.24	0.02	0.53	0.44	38.1	0.79	
	CH	0.53 $\pm$ 0.27	0.40	0.41	0.53	35.4	1.14	
	CI	0.45 $\pm$ 0.23	0.45	0.33	0.58	35.6	1.40	
	SI	0.54 $\pm$ 0.29	0.10	0.60	0.75	46.6	2.58	
	SE	0.49 $\pm$ 0.25	0.11	0.55	0.51	39.5	1.29	
	VE	0.35 $\pm$ 0.12	0.19	0.52	0.52	40.8	0.80	
	VI	0.49 $\pm$ 0.24	0.08	0.50	0.30	27.4	0.65	
DMin	LA	0.46 $\pm$ 0.05	0.43	0.07	0.73	44.0	3.04	
	LU	0.45 $\pm$ 0.04	0.48	0.06	0.89	56.0	8.02	
	AR	0.46 $\pm$ 0.06	0.36	0.07	0.83	48.9	4.94	
	BU	0.41 $\pm$ 0.06	0.39	0.07	0.77	38.5	3.29	
	CH	0.40 $\pm$ 0.04	0.45	0.06	0.78	39.9	3.49	
	CI	0.43 $\pm$ 0.06	0.43	0.07	0.80	39.5	4.09	
	SI	0.41 $\pm$ 0.05	0.21	0.07	0.82	46.0	4.21	
	SE	0.49 $\pm$ 0.07	0.18	0.10	0.84	49.5	5.02	
	VE	0.46 $\pm$ 0.05	0.45	0.09	0.85	50.7	5.12	
	VI	0.47 $\pm$ 0.05	0.46	0.09	0.87	53.7	5.87	
DMax	LA	0.63 $\pm$ 0.06	0.64	0.05	0.82	32.8	0.45	
	LU	0.61 $\pm$ 0.06	0.46	0.05	0.73	31.4	2.73	
	AR	0.65 $\pm$ 0.07	0.60	0.05	0.58	34.3	0.92	
	BU	0.60 $\pm$ 0.07	0.46	0.05	0.76	39.2	3.20	
	CH	0.58 $\pm$ 0.06	0.63	0.05	0.61	38.3	1.55	
	CI	0.63 $\pm$ 0.07	0.64	0.05	0.57	32.3	0.87	
	SI	0.64 $\pm$ 0.06	0.49	0.05	0.78	42.3	3.50	
	SE	0.71 $\pm$ 0.08	0.39	0.06	0.65	38.0	1.85	
	VE	0.66 $\pm$ 0.07	0.40	0.06	0.40	38.5	1.66	
	VI	0.67 $\pm$ 0.07	0.37	0.06	0.44	34.1	0.77	

Abbreviations: SD, standard deviation; AC, first-order autocorrelation; MS_x, mean sensitivity; EPS, expressed population signal; PC1, variance explained by the first principal component; SNR, signal to noise ratio.

Figure legends

Figure 1. Location of *J. thurifera* study sites in the Iberian Peninsula and geographical variability of May precipitation (shown as a colour background map, which was built using the Digital Climatic Atlas of the Iberian Peninsula; see Ninyerola et al. 2000). The different symbols of the study sites indicate the four geographical groups of sites based on growth variability (see also DeSoto *et al.* 2012). Site codes are as in Table 1.

Figure 2. Illustration of *J. thurifera* tree-ring wood anatomy in transversal section (upper image) and related intra-annual variability of the density (lower figure). The density profile (black line) corresponds to a typical *J. thurifera* ring as shown in the upper figure, in which the maximum (DMax) and minimum (DMin) values are indicated as red and blue symbols, respectively. The grey lines with symbols show the intra-annual variability (grey scale) of tracheid lumen and wall density, as seen in an image taken using a light microscope.

Figure 3. Site chronologies (gray lines) of the four selected variables and means for all sites (black lines). Variables are abbreviated as in Table 2. The percentage of growth variance of the ten site chronologies, accounted for by the first principal component (PC1), is shown for each variable.

Figure 4. Correlation coefficients calculated between site chronologies versus inter-site distance considering different variables (DMax, maximum wood density; DMin, minimum wood density; EW, earlywood width; LW, latewood width). The amount of variance explained by distance (r^2) is indicated for each variable. Points located outside the gray boxes indicate significant coefficients ($P < 0.05$).

Figure 5. Relationships between earlywood (EW) and latewood (LW) width chronologies and monthly climatic variables (Tmin and Tmax, mean minimum and maximum temperatures; Prec, precipitation; PDSI, self-calibrated Palmer Drought Severity Index). The different colours of symbols indicate regional groups of sites based on their similar growth variability and geographical location (see Fig. 1). Significant correlation coefficients ($P < 0.05$) are those located outside the gray boxes. Correlations were calculated from the previous (months abbreviated by lowercase letters) up to the current September (months abbreviated by uppercase letters).

Figure 6. Relationships between maximum (DMax) and minimum (DMin) wood density site chronologies and monthly climatic variables (Tmin and Tmax, mean minimum and maximum temperatures; Prec, precipitation; PDSI, self-calibrated Palmer Drought Severity Index). The rest of explanations are as in Figure 5.

Figure 7. Temporal relationships between the composite series (means of site chronologies) of maximum wood density, minimum wood density and the precipitation sums most tightly related to them (note the reverse scales of precipitation data). The correlations between the variables (r), and their significances (P), are indicated in the lower left corner of each graph.

Figure 8. Geographic patterns of the major climatic drivers of *J. thurifera* minimum density (a, May precipitation; b, May mean maximum temperature; c, June PDSI). The size of circles is proportional to the absolute correlation value between minimum density and the corresponding climatic variable (see also Figure 6). Underlined codes indicate significant correlation coefficients ($P < 0.05$). The colour underground corresponds to May

precipitation. Sites' codes are shown in Table 1.

Figure 9. Spatial correlations calculated between the composite *J. thurifera* chronology of minimum density across its Iberian range and two (0.5°-gridded) climatic variables: May mean maximum temperatures (a) and June PDSI (b). The colour scale indicates Pearson correlation values and the presented patterns are globally significant at $P < 0.01$ for the analysed area (South Western Europe and North Western Africa) and period (1951–2000). The symbols indicate the approximate location of the study sites (see Figure 1).

Figures

Figure 1

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