

# Influence of drought on tree rings and tracheid features of *Pinus nigra* and *Pinus sylvestris* in a mesic Mediterranean forest

Dario Martin-Benito · Hans Beeckman ·  
Isabel Cañellas

Received: 18 January 2012/Revised: 2 June 2012/Accepted: 30 July 2012  
© Springer-Verlag 2012

**Abstract** We investigated the influence of climate on the ring width and xylem anatomy of two co-occurring pines (*Pinus nigra* Arn. and *P. sylvestris* L.) in the mountains of east-central Spain in order to test their utility for dendroclimatic reconstructions. We developed chronologies of ring width, mean lumen diameter and mean cell-wall thickness (in the earlywood, latewood, and the total annual ring) and the number of cells between 1960 and 2006. Drought, expressed as the standardized precipitation-evapotranspiration index (SPEI), was the main climatic driver of tree radial growth, although trees were also sensitive to temperature (negative effect in previous autumn and current summer) and precipitation (with a general positive effect). *P. sylvestris* response was stronger to climate of the current year, whereas the effect of previous-year climate was more important for *P. nigra*. Warm and dry summers reduced ring width, tracheid lumen, and wall thickness in both species, whereas warm winter-spring temperatures had the opposite effect, primarily for *P. sylvestris*.

Previous-year or early-season conditions mainly affected earlywood features, whereas latewood was more responsive to summer climate. Overall, climate appeared to be a stronger limiting factor for *P. sylvestris*. During periods of drought, cell-wall thickness was reduced while lumen width increased in the latewood of *P. sylvestris*. This could compromise its hydraulic safety against drought-induced cavitation as our site was close to the southern and dry edge of the species distribution area. Our results suggest that anatomical variables record different and stronger climate information than ring width variables, especially in *P. sylvestris*. Reconstruction models for SPEI at the 3-month scale were developed for July–August and September–October using principal components regression. The best models included anatomical and width variables of both pine species suggesting that tracheid chronologies can be useful for drought reconstructions especially at mesic sites or with species that encode a mixed drought and temperature-precipitation signal.

Communicated by R. Matyssek.

D. Martin-Benito (✉)  
Tree-ring Laboratory, Lamont-Doherty Earth Observatory  
of Columbia University, 61 Route 9 W, Palisades,  
NY 10964, USA  
e-mail: dmbenito@ldeo.columbia.edu;  
dmartinbenito@gmail.com

H. Beeckman  
Laboratory for Wood Biology and Xylarium, Royal Museum for  
Central Africa, Leuvensesteenweg 13, 3080 Tervuren, Belgium  
e-mail: hans.beeckman@africamuseum.be

I. Cañellas  
Dpte. of Silviculture and Forest Management, INIA, Forest  
Research Centre, Avd. A Coruña km.7.5, 28040 Madrid, Spain  
e-mail: canellas@inia.es

**Keywords** Dendrochronology · Drought · Xylem · Wood anatomy · Climate reconstruction · Scots pine · Black pine

## Introduction

The annual growth rings of trees are a valuable source of environmental information and have been widely used for paleoclimate reconstructions with annual resolution throughout the world. The reconstructed climate variables have generally been the most limiting climatic factor for tree growth. In cold environments such as high altitudes or latitudes, successful reconstructions of summer temperatures have been possible (e.g., D'Arrigo et al. 2006; Esper et al. 2002; Cook et al. 2004), whereas in warmer climates,

drought indices have generally been the reconstructed variables (Nicault et al. 2008; Cook et al. 2010). In these climate reconstructions, tree-ring width has been the most commonly used proxy followed by maximum ring density (Hughes 2002). However, in climates with multiple limiting climatic factors or with no dominant factor (e.g., mesic sites in dry climates), the climate signal recorded in tree rings might be mixed or weak.

In the Mediterranean climate, cold winter temperatures and summer drought limit growth (i.e., double stress), and summer and winter temperatures usually have opposite effects (negative and positive, respectively) on tree growth (Gea-Izquierdo et al. 2011; Martín-Benito et al. 2010; Andreu et al. 2007) while the effect of cumulative precipitation before growth resumes in spring can be more important than summer precipitation (Piovesan et al. 2008). These opposite or cumulative effects can be obscured in tree-ring width series, and the climatic signal might be better recorded by cell development processes. This region is therefore very promising to study intra-annual influence of climate upon plant growth through the analysis of wood anatomical features (Cherubini et al. 2003; Fonti et al. 2010).

In conifers, where wood is mainly composed of tracheids, ring features result from the accumulation of three processes: cambial division (the number of cells formed), cell expansion (determines lumen diameter), and cell-wall thickening. Because these processes are influenced by different factors at or before their time of formation (e.g., Deslauriers and Morin 2005; Attolini et al. 1990; Gindl et al. 2000; Donaldson 2002), their anatomical structure encodes information on these environmental factors. The effect of climatic conditions might be different for each of these processes that might make it convenient to separately analyze the climate signal recorded in wood anatomical features within the annual growth ring (Fonti et al. 2010 and references therein).

In general, time series of tracheid anatomical features have been scarcely used to analyze their environmental signal despite several studies showing their dendroclimatic potential in temperate and cold climates (Panyushkina et al. 2003; Yasue et al. 2000; Wang et al. 2002; Kirilyanov et al. 2003; Eilmann et al. 2009; Wimmer and Grabner 2000). The best results have been found between latewood anatomy (mainly cell-wall thickness) and summer temperatures (Panyushkina et al. 2003; Yasue et al. 2000; Wang et al. 2002; Kirilyanov et al. 2003) or both temperature and precipitation (Eilmann et al. 2009; Wimmer and Grabner 2000). Some of these studies also reported maximum ring density to be a similar or better climate proxy than cell-wall thickness (Yasue et al. 2000; Wang et al. 2002; Wimmer and Grabner 2000). Recently, several studies have concluded that vessel features in the

annual rings of Mediterranean oaks record stronger precipitation signal (Campelo et al. 2010) or have a different seasonal signal (Gea-Izquierdo et al. 2012) than ring width. However, no studies to date have explored the climatic signal recorded in the time series of tracheid features of conifers growing under Mediterranean climate.

In the Mediterranean basin, as temperature increases and precipitation decreases, drought spells are expected to intensify (Meehl and Tebaldi 2004) which will greatly influence different physiological and anatomical processes in trees regarding their hydraulic conductance (Cinnirella et al. 2002; Irvine et al. 1998). The double function of tracheids, that is, for water conduction and structural support, requires a trade-off between wide thin-wall cells for water transport and small thick-wall cells for support (Hacke and Sperry 2001). Thicker walls are also needed to withstand the negative pressures caused by water stress (Hacke and Sperry 2001; Pittermann et al. 2006). During periods of water stress, stomata close to reduce water loss, maintain internal water balance, and prevent xylem cavitation (Irvine et al. 1998), which limits gas interchange, reduces carbon uptake and eventually growth (Jones 1998). Trees also respond by adjusting carbon allocation, usually allocating more carbon to reserves (Wiley and Helliker 2012) and favoring root development against aboveground growth (Dewar et al. 1994). These factors combined with a reduced sink activity (Körner 2003) might compromise cell-wall thickening. The necessary trade-offs between these physiological and wood anatomical processes as an adaptation to different environments might define in part the distributional limits of many conifer species (Brodrick and Hill 1999).

In recent years, mortality of Scots pine (*Pinus sylvestris* L.) in some of its more southern populations has been related to increasing aridity (Navarro Cerrillo et al. 2007), whereas black pine (*P. nigra* Arn.) was not affected (Martínez-Vilalta and Piñol 2002). Black pine is a pan-Mediterranean species with a wide distribution range, from the Iberian Peninsula to Turkey and from Northern Africa to Austria (Barbéro et al. 1998) while Scots pine is a boreal pine considered to be the most widely distributed conifer in the world extending from the Iberian Peninsula to Siberia (Nikolov and Helmisaari 1992). In eastern Spain, Scots pine occupies the highest (up to 2,000 m asl) and more mesic sites above black pine which forms forests at intermediate altitudes above the more thermophilic pines (*P. halepensis* Mill., *P. pinea* L., *P. pinaster* Ait.) (Barbéro et al. 1998). In the Iberian Mountain Range (east-central Spain), black pine and Scots pine frequently form mixed forests that are close to the southern distribution limit of Scots pine forests but at the ecological optimum for black pine (Barbéro et al. 1998). The co-occurrence of these two species, with contrasting resistance to drought, allows for

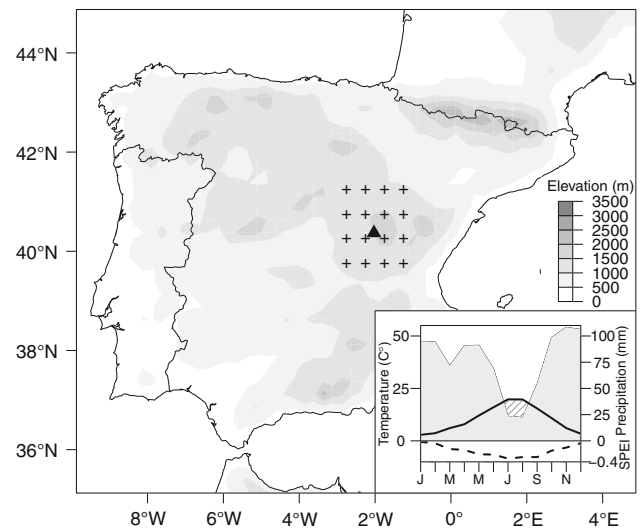
the comparison of the response of tree-ring growth and anatomical characteristics of xylem to climate under the same environmental conditions.

In this study, we explore the climate response of anatomical features in the tree rings of black pine and Scots pine for a mesic Mediterranean site and their potential as proxies for paleoclimate reconstructions. The specific objectives of this study were (1) to analyze whether there is a climatic signal recorded in time series of tracheid sizes of the two pine species, (2) determine whether these features show stronger correlations with climate or provide different temporal resolution than the more commonly used ring width, and (3) examine the possible advantages of combining ring width and tracheid size chronologies for the two species as climate proxies. We hypothesize that tracheid dimensions record a stronger signal than ring width variables because they are affected by climate at shorter time scales. We also anticipate Scots pine to be more sensitive to climate, particularly drought, because our study site is close to its southern distribution limit.

## Materials and methods

### Site description

The study area is located on the Iberian Mountain range in east-central Spain with latitude of 40°17'N, longitude of 1°59'W, and at an altitude of 1,460 m a.s.l. It is a mixed even-aged (ca. 90 years old) stand of black (*Pinus nigra* Ait.) and Scots pine (*P. sylvestris* L.) on a well-developed and deep forest soil on calcareous bedrock and flat slope. The climate is Mediterranean with two precipitation maxima in spring and autumn and a drought period of about 2 months in July and August (Fig. 1). Total mean annual precipitation for the period 1970–2000 was 924 mm, and the mean temperature was 13.3 °C (Fig. 1). Precipitation and temperature data were provided by the Spanish National Meteorological Agency (AEMET) for the nearby 'La Toba' meteorological station located at 1250 m asl (40°13'N; 1°55'W; about 10 km southwest of the sampling site). In addition, we used a multiscale climatic drought index, the standardized precipitation-evapotranspiration index (SPEI), (Vicente-Serrano et al. 2010) that unlike the standardized precipitation index (SPI) includes the effect of temperature on its calculation. Time series of 0.5° × 0.5° gridded SPEI at time scales between one and 24 months (available at: <http://sac.csic.es/spei/download.html>) were analyzed for their correlation with ring chronologies. We produced average SPEI time series for each time scale for the 16 SPEI grid points closest to the study site between 1.25°–2.75°W and 39.75°–41.25°N (Fig. 1).



**Fig. 1** Map of the study region in Spain showing the locations of the sampling site and meteorological station (black triangle; 40°24'N, 2°5'W), and the 16 grid points used for the average value of SPEI. Climate diagram shows monthly mean temperature (solid line; left axis), total precipitation (gray area; right axis), and SPEI (dashed line; bottom right axis)

### Dendrochronological and wood anatomical methods

For each species, we extracted two cores from each of the selected 15 dominant trees (30 trees in total) within a permanent sample plot of 2,000 m<sup>2</sup>. Trees dominance was defined as the 100 largest diameter trees per hectare (Assmann 1970). Cores were mounted on grooved boards, sanded, and crossdated (Stokes and Smiley 1968). Total ring width (TRW), earlywood width (EW), and latewood width (LW) were measured to the nearest 0.01 mm with a LINTAB measuring table using the TSAP software (Rinntech, Heidelberg, Germany). Crossdating and data quality were validated using the COFECHA program (Holmes 1983). After tree-ring raw width chronologies were built, we selected for the wood anatomical analysis a subset of the five trees per species that best matched their species mean chronology. Cores were removed from the grooved boards and dehydrated in several steps of different ethanol concentrations. Core sections for the period 1960–2006 were cut into smaller parts (1–2 cm) and embedded in polyethylene glycol of 1,500 MW (PEG) to form small blocks (Schmitz et al. 2007). Sections 20 μm thick were then cut from these blocks with a sliding microtome, dehydrated, and mounted onto non-permanent glass microscope slides.

Digital images of the thin sections were taken with a magnification of 40× using a CCD video camera installed on an optical microscope (Nikon Eclipse E600). UV-reflected light was used (mercury vapor lamp with an

U-MWU Olympus filter) because the autofluorescence of lignin creates very high contrast between light cell walls and dark background (Donaldson 2002). A total of 235 tree rings (5 trees  $\times$  47 rings per tree) were analyzed for each species. For wide rings (i.e., width  $>500 \mu\text{m}$ ), successive images were merged into a single mosaic image. In each ring, radial lumen diameter (LD), radial cell-wall thickness (CWT), and number of cells (NC) were semi-automatically measured along five complete radial rows of cells using the ImageJ software (Rasband 1997) with a resolution of 1,430 pixels/ $\mu\text{m}$ . Radial dimensions were chosen because tangential tracheid sizes can be assumed to be practically constant (Vysotskaya and Vaganov 1989).

For each individual tracheid, CWT was calculated with the formula by Filion and Cournoyer (1995):  $CWT_i = 0.5 \cdot (CWT_{i-1} + CWT_{i+1})$ , where  $CWT_{i-1}$  and  $CWT_{i+1}$  represent the distance between left ( $i - 1$ ) and right ( $i + 1$ ) side tracheid lumen to the specific tracheid ( $i$ ), respectively. In the case of first and last tracheids in a tree ring, the formula was modified to  $CWT_{\text{first}} = CWT_{i+1}$  and  $CWT_{\text{last}} = CWT_{i-1}$ . Total tracheid diameter (TD) was computed as  $TD_i = 0.5 \cdot CWT_{i-1} + LD_i + 0.5 \cdot CWT_{i+1}$ .

The first latewood cell was defined as the cell in which  $CWT-4 \geq LD$  (Filion and Cournoyer 1995). All cells after the first latewood cell were considered latewood. Based on TD in individual files, the percentage of latewood (LP) was computed as

$$LP = 100 \cdot \frac{\sum_{j=1}^n TD_j}{\sum_{i=1}^N TD_i}$$

where  $n$  and  $N$  are the number of latewood cells and total number of cells in each tree ring, respectively.

Times series were built for the mean anatomical variables of each year and tree and for both earlywood and latewood. In order to reduce the number of redundant chronologies, we checked the correlations among chronologies of anatomical features in each species. Variables that were highly correlated with each other were not used for growth-climate analysis [mean tracheid area (A) and tracheid mean diameter (TD)] but were nonetheless compared between species. Thus, we only considered time series of cell lumen diameter (LD) and cell-wall thickness (CWT) in earlywood and latewood and mean number of cells (NC) in each tree ring (Table 1). We also included

**Table 1** Descriptive statistics for residual chronologies of anatomical and ring width variables for the period 1960–2006 for *Pinus nigra* (Pini) and *P. sylvestris* (Pisy)

Variable	Mean <sup>1</sup>		SD		MS		AC		EPS		Rbar	
	Pini	Pisy	Pini	Pisy	Pini	Pisy	Pini	Pisy	Pini	Pisy	Pini	Pisy
A ( $\mu\text{m}^2$ )*	656.98 a	576.49 a	85.26	66.22	0.19	0.17	0.18	0.28	0.77	0.70	0.40	0.32
EA ( $\mu\text{m}^2$ )*	919.19 a	769.13 b	90.31	53.56	0.12	0.11	0.31	0.39	0.64	0.25	0.26	0.06
LA ( $\mu\text{m}^2$ )*	107.34 a	111.62 a	22.04	30.01	0.32	0.35	0.03	0.07	0.47	0.77	0.15	0.41
CWT ( $\mu\text{m}$ )	4.58 a	3.68 a	0.63	0.43	0.19	0.16	0.19	0.33	0.81	0.79	0.47	0.42
CWE ( $\mu\text{m}$ )	3.77 a	3.19 a	0.39	0.35	0.14	0.13	0.40	0.41	0.49	0.62	0.16	0.25
CWL ( $\mu\text{m}$ )	6.08 a	4.58 b	0.84	0.59	0.21	0.21	0.07	0.18	0.83	0.82	0.50	0.48
LD ( $\mu\text{m}$ )	25.82 a	23.92 a	2.29	2.14	0.12	0.12	0.14	0.16	0.82	0.81	0.48	0.45
LDE ( $\mu\text{m}$ )	34.45 a	30.55 b	2.43	1.87	0.09	0.08	0.17	0.22	0.79	0.63	0.43	0.26
LDL ( $\mu\text{m}$ )	8.02 a	8.10 a	0.96	1.37	0.19	0.22	0.06	0.03	0.57	0.81	0.21	0.46
LP (%)	18.44 a	16.80 a	0.05	0.06	0.47	0.64	0.03	-0.02	0.83	0.84	0.49	0.51
NC (cells)	21.16 a	25.58 a	7.27	7.73	0.33	0.27	0.45	0.56	0.89	0.86	0.62	0.55
TD ( $\mu\text{m}$ )*	30.36 a	27.59 b	2.13	2.11	0.11	0.10	0.30	0.18	0.76	0.82	0.38	0.47
TDE ( $\mu\text{m}$ )*	38.22 a	33.75 b	2.56	2.02	0.09	0.08	0.14	0.25	0.77	0.67	0.41	0.28
TDL ( $\mu\text{m}$ )*	13.95 b	12.60 b	1.48	1.72	0.14	0.19	0.13	0.00	0.79	0.83	0.43	0.50
TRW (mm)	1.38 a	1.20 a	1.17	0.86	0.33	0.30	0.77	0.75	0.89	0.90	0.43	0.46
EW (mm)	1.11 a	0.99 a	1.02	0.78	0.36	0.33	0.77	0.73	0.88	0.90	0.41	0.44
LW (mm)	0.27 a	0.21 a	0.19	0.13	0.43	0.45	0.54	0.36	0.90	0.89	0.44	0.43

Variables abbreviations are: A tracheid area, EA earlywood tracheid area, LA latewood tracheid area, CWT, CWE, and CWL tracheid cell-wall thickness for the ring, earlywood, and latewood, respectively; LD, LDE, and LDL, tracheid lumen diameter for the ring, earlywood, and latewood, respectively; LP percentage of latewood, NC number of cells, TD, TDE, and TDL tracheid diameter for the ring, earlywood, and latewood, respectively; TRW tree-ring width, EW earlywood width, LW latewood width. Asterisk denote variables that were removed from further analysis (see text)

<sup>1</sup> Means with different letters indicate significant differences between species ( $p < 0.05$ )

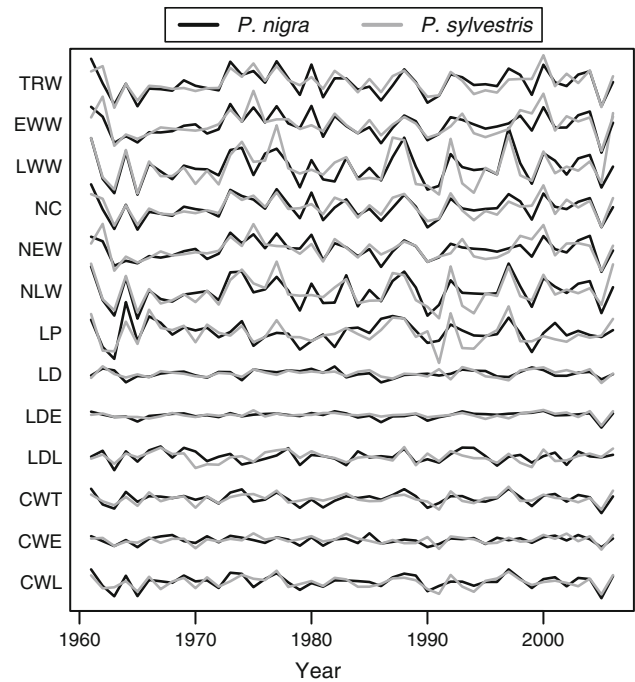
SD standard deviation, MS mean sensitivity, AC first-order autocorrelation, EPS expressed population signal, Rbar running mean inter-series correlation

series of tree-ring width (TRW), earlywood width (EWW), latewood width (LWW), and percentage of latewood (LP). Time series for each variable and species were standardized with a negative exponential function, a very conservative detrending, and using the library ‘dplR’ (Bunn 2008) in the R program (R Development Core Team 2008). Dimensionless indexes were computed by dividing observed values by the estimated values of the fitted curves and autocorrelation removed to produce residual chronologies. For each standardized chronology, standard dendrochronological statistics such as first-order autocorrelation (AC1), mean sensitivity (MS), and expressed population signal (EPS) were computed.

Statistical analyses and dendroclimatic reconstructions

Principal component analysis (PCA) and redundancy analysis (RDA) were used to explore the relationship among anatomical and ring width chronologies and between those and climate variables, respectively. RDA has been widely used in dendrochronology to analyze the climatic signal in ring width and wood anatomical variables (e.g., Tardif and Conciatori 2006; Beeckman and Van der Mijnsbrugge 1993). RDA is the multivariate analogy of multiple regression assuming linear relationships between response (tree-ring variables) and explanatory variables (climate variables) (Legendre and Legendre 1998). For the selection of significant variables ( $\alpha < 0.05$ ), forward selection with 10,000 Monte Carlo permutations was used. PCA and RDA were conducted in the package ‘vegan’ (Oksanen et al. 2008) in the R program (R Development Core Team 2008) using correlation matrixes because the developed chronologies (ring width and anatomical features) were not scaled to the same variance (Fig. 2). We also calculated simple Pearson correlation coefficients between chronologies and climate variables time series.

In order to evaluate the potential use of chronologies of tracheid features for climate reconstructions, we developed several models of SPEI with three combinations of variables (1) all variables, (2) width variables only (TRW, EWW, and LWW), and (3) anatomical variables only, by means of principal component regression (PCR) modeling (Cook et al. 1999). These groups of variables were considered for each species separately and for both species together to analyze the effect of combining ring features and different species. Principal component analysis was used to convert original chronologies into orthogonal PCs, which eliminates multicollinearity caused by high correlation between tree-ring chronologies (Table 2). The resulting PCs (lagged -1, 0, and 1 years) were then used in a multiple regression model as predictors of SPEI. The best subsets of PCs retained in the final models were determined according to the minimum Akaike information criterion



**Fig. 2** Residual chronologies for *Pinus nigra* (black line) and *P. sylvestris* (gray line) anatomical and ring variables for the period 1960–2006. See Table 1 for variable abbreviations

**Table 2** Pearson’s correlation coefficients for cell and tree-ring dimension chronologies

Variable	<i>P. nigra</i>			<i>P. sylvestris</i>		
	TRW	LW	EW	TRW	LW	EW
TRW						
LW	<b>0.78</b>			<b>0.67</b>		
EW	<b>0.98</b>	<b>0.64</b>		<b>0.98</b>	<b>0.50</b>	
NC	<b>0.97</b>	<b>0.82</b>	<b>0.93</b>	<b>0.96</b>	<b>0.75</b>	<b>0.90</b>
LP	<b>0.29</b>	<b>0.73</b>	0.12	-0.06	<b>0.55</b>	-0.22
LD	0.19	<b>-0.30</b>	<b>0.33</b>	<b>0.37</b>	-0.23	<b>0.51</b>
LLD	<b>0.28</b>	<b>0.34</b>	0.24	0.22	<b>0.57</b>	0.09
ELD	<b>0.54</b>	<b>0.35</b>	<b>0.55</b>	<b>0.63</b>	<b>0.27</b>	<b>0.66</b>
CWT	<b>0.67</b>	<b>0.86</b>	<b>0.55</b>	<b>0.58</b>	<b>0.76</b>	<b>0.46</b>
CWL	<b>0.61</b>	<b>0.84</b>	<b>0.48</b>	<b>0.44</b>	<b>0.75</b>	<b>0.29</b>
CWE	<b>0.71</b>	<b>0.58</b>	<b>0.68</b>	<b>0.60</b>	<b>0.41</b>	<b>0.58</b>

Variable abbreviations are the same as in Table 1. Significant coefficients ( $p < 0.05$ ) appear in bold

(AIC; Akaike 1974). Because of the short time span of our chronologies, we used the entire period (1960–2006) for the model calibration. Model verification was performed using a jackknife approach, leaving one observation out at each step, with which verification statistics, namely reduction of error (RE) and Spearman correlation coefficients between observed and estimated SPEI, were calculated. In total, 18 models were compared. Mean July–August

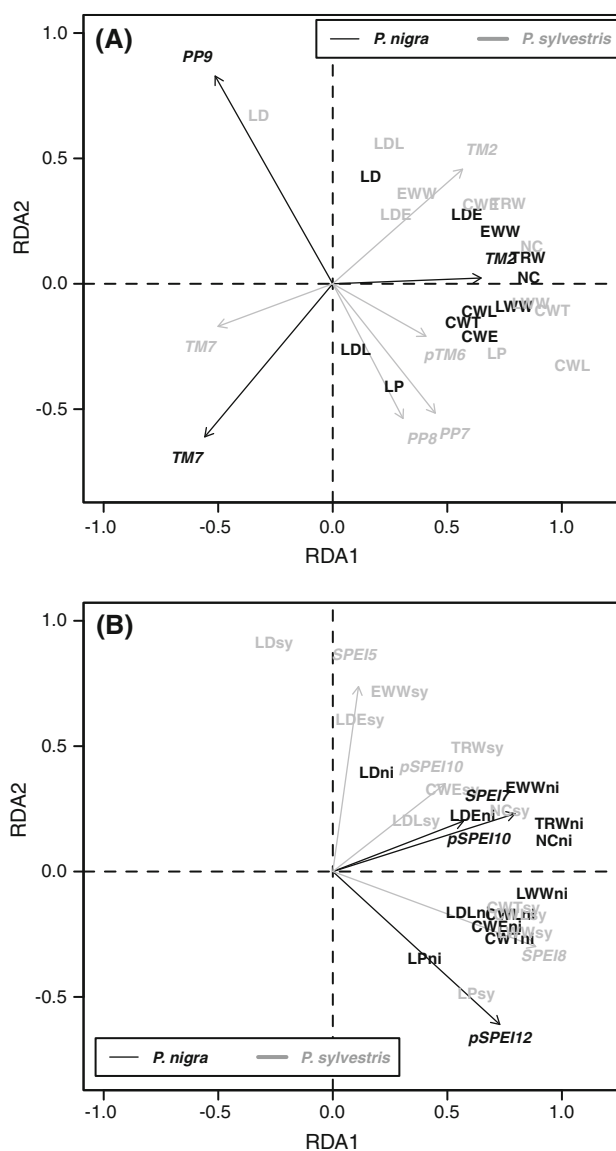
(JA) and September–October (SO) SPEI were selected for reconstruction based on our results from the RDA and Pearson correlations. In addition, we analyzed the performance of our models in spatial field correlations between observed and predicted JA and SO SPEI in southwestern Europe and northwestern Africa for the period 1960–2006.

## Results

### Anatomy and chronology characteristics

Cell radial dimensions were very similar for both pine species. Mean tracheid lumen diameter (LD) was wider in black pine (25.82  $\mu\text{m}$ ) than in Scots pine (23.92  $\mu\text{m}$ ) mainly because of wider earlywood tracheids (LDE; 34.45 and 30.55  $\mu\text{m}$ , respectively) (Table 1). The thicker cell walls in black pines (4.58  $\mu\text{m}$ ) compared to those of Scots pine (3.68  $\mu\text{m}$ ) were caused by differences in latewood cell-wall thickness (CWL; 6.08 and 4.58  $\mu\text{m}$ , respectively). Dendrochronological statistics were also very similar in both pines (Table 1) and showed that percentage of latewood (LP) had the highest mean sensitivity (MS). Ring width variables (total ring, earlywood, and latewood width) had higher MS and first-order autocorrelation (AC) than anatomical chronologies (Table 1). In general, all latewood-related variables showed higher MS and lower AC than corresponding variables in earlywood or the entire ring also supported by the greater inter-annual variability observed in latewood variables (Fig. 3). However, this difference was not observed for the expressed population signal (EPS) or the running mean inter-series correlation (Rbar) (Table 1). EPS was above 0.85 in ring width variables (TRW, EWW, and LWW) and number of cells (NC). Anatomical chronologies were less influenced by previous-year growth than ring width variables as shown by their lower AC.

In the principal component analysis (PCA), each of the 11 pairs of variables of the two species appeared close to each other, thus further supporting few differences between black pine and Scots pine (Fig. 3). PC1 and PC2 represented 38.3 and 27.4 % of the variance, respectively. The first two PCs clearly segregated chronologies between those in the latewood (e.g., percentage of latewood or latewood cell-wall thickness) on the positive side of PC2 from total ring or earlywood variables (e.g., ring width or number of cells) on the negative values of PC2. Correlations between different ring and anatomical variables further corroborated these results (Table 2). As an expected result, latewood width of both pines was negatively correlated with lumen diameter and positively correlated with cell-wall thickness (Table 2) suggesting that rings with



**Fig. 3** Redundancy analysis (RDA) calculated for anatomical and ring width variables for the period 1960–2005, and **a** monthly climate variables (precipitation and temperature), and **b** drought index SPEI. See Table 1 for variables abbreviations. In RDA, the loading of the variables or the length of the vector indicates the strength of the correlation with the ordination axis. Vectors of climate variables pointing in the same direction that anatomical or width features indicate a high positive correlation, vector pointing at right angles indicate no correlation, and vectors pointing in opposite directions indicate high negative correlations (Ter Braak 1994) and are significant at  $p < 0.05$ . Monthly climate variables are monthly precipitation (e.g., PP5 for May of the current year; pPP10 for October of the year before ring formation) and mean temperature (e.g., TM6 for June)

wider latewood also have a larger percentage of their section occupied by cell-wall and less area occupied by tracheid lumens. Tree-ring width was also positively correlated with the mean number of cells in both pines (Table 2). Black pine had wider rings for the same number

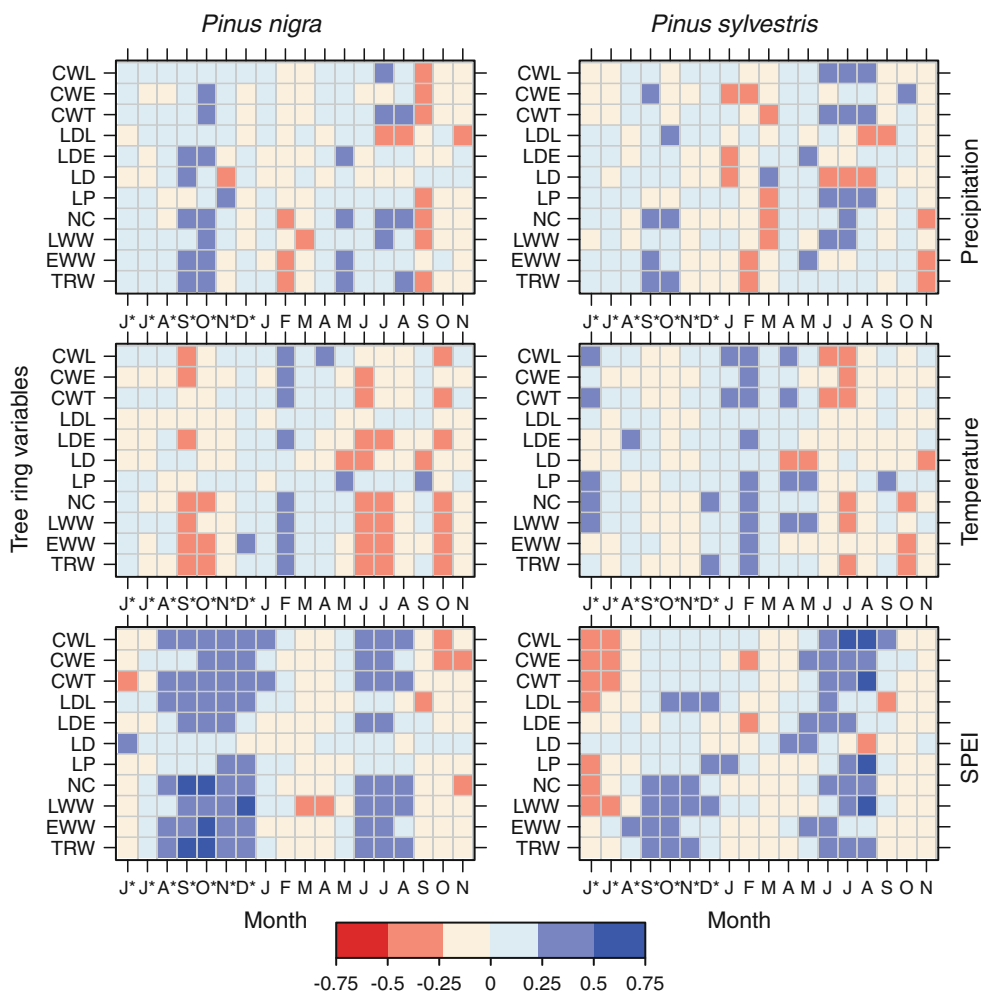
of cells than Scots pine as a consequence of black pine having larger lumen diameters and thicker cell walls (Table 1).

Relationship between chronologies and climate variables

All width and anatomical variables showed significant correlations with precipitation, temperature, or SPEI. These associations between climate variables and ring chronologies revealed important similarities and differences between black pine and Scots pine (Figs. 3, 4). Earlywood variables were more affected by previous-year climate, whereas latewood variables showed greater association with current year conditions. For both pine species, precipitation during previous fall and current spring and summer was beneficial for ring growth, particularly earlywood development (earlywood width, cell-wall thickness, and lumen diameter). However, low water availability (precipitation and SPEI) during the current summer caused Scots pine to produce fewer tracheids with wider lumen diameters but thinner walls throughout the entire ring.

These effects were stronger for latewood variables, which reduced latewood width and the proportion of the ring covered by latewood as drought increased. Simple correlations with water availability showed effects on black pine growth that were opposite between summer (July and August) and autumn (September) of the current year (Fig. 4) although these relationships were not shown in the RDA (Fig. 3). High precipitation and SPEI in the summer (autumn) had a positive (negative) correlation with ring width, the number of cells produced, and cell-wall thickness. In both pines, warm winter temperatures before growth enhanced ring growth, whereas current summer temperatures (mainly July) had a negative effect. Black pine showed greater sensitivity to temperatures as previous autumn and current summer temperatures decreased growth more than in Scots pine, which mainly reacted to high temperatures by producing fewer latewood cells with thinner walls (Fig. 4). In both pine species, the highest correlations between ring variables and climate were found for the drought index SPEI (Fig. 4), which incorporates the effect of precipitation and temperature. Overall, black pine showed a greater influence of climate the previous year

**Fig. 4** Pearson correlation coefficients between *P. nigra* and *P. sylvestris* chronologies and monthly climatic variables for the period 1960–2006. The two darker shades of blue (red) show the positive (negative) significant correlations ( $p < 0.05$ ). Lighter blue and orange denote positive and negative non-significant correlations. To the left of each panel, asterisk denotes months of the year before tree-ring formation ( $t - 1$ ). (Color figure online)



**Table 3** Calibration (1960–2006) and verification statistics for the principal component multiple regression models developed to estimate mean SPEI for July–August (JA) and September–October (SO) from tree-ring features

Species	Variables	$R^2$	Adjusted $R^2$	$r$	SE	RMSE	RE	Model
JA								
<i>P. nigra</i>	<b>All</b>	<b>0.36</b>	<b>0.31</b>	<b>0.60</b>	<b>0.7871</b>	<b>0.7871</b>	<b>0.2238</b>	<b>PC1 + PC3 + PC3<sub>(t-1)</sub></b>
<i>P. sylvestris</i>								
	Width	0.33	0.28	0.57	0.7979	0.7979	0.2025	PC1 + PC2 + PC3 <sub>(t-1)</sub>
	Anatomy	0.31	0.28	0.56	0.8004	0.8004	0.1974	PC1 + PC3
<i>P. nigra</i>	All	0.21	0.17	0.45	0.8542	0.8542	0.0860	PC1 + PC3
	Width	0.26	0.21	0.51	0.8449	0.8449	0.1057	PC1 + PC1 <sub>(t-1)</sub> + PC3 <sub>(t+1)</sub>
	Anatomy	0.17	0.13	0.41	0.8746	0.8746	0.0416	PC1 + PC3
<i>P. sylvestris</i>	All	0.31	0.28	0.56	0.8049	0.8049	0.1884	PC1 + PC2
	Width	0.27	0.22	0.52	0.8544	0.8544	0.0855	PC1 + PC2 + PC2 <sub>(t-1)</sub>
	Anatomy	0.31	0.29	0.55	0.7863	0.7863	0.2254	PC1
SO								
<i>P. nigra</i>	<b>All</b>	<b>0.45</b>	<b>0.40</b>	<b>0.67</b>	<b>0.7436</b>	<b>0.7436</b>	<b>0.3366</b>	<b>PC1<sub>(t+1)</sub> + PC1<sub>(t-1)</sub> + PC3 + PC3<sub>(t-1)</sub></b>
<i>P. sylvestris</i>								
	Width	0.33	0.30	0.57	0.7957	0.7957	0.2404	PC1 <sub>(t-1)</sub> + PC3 <sub>(t-1)</sub>
	Anatomy	0.39	0.33	0.63	0.7767	0.7767	0.2763	PC1 <sub>(t+1)</sub> + PC1 <sub>(t-1)</sub> + PC3 + PC3 <sub>(t-1)</sub>
<i>P. nigra</i>	All	0.42	0.35	0.65	0.7909	0.7909	0.2495	PC1 <sub>(t+1)</sub> + PC1 <sub>(t-1)</sub> + PC3 + PC3 <sub>(t-1)</sub> + PC3 <sub>(t-1)</sub>
	Width	0.32	0.30	0.57	0.7860	0.7860	0.2589	PC1 <sub>(t-1)</sub>
	Anatomy	0.39	0.31	0.62	0.8095	0.8095	0.2138	PC1 <sub>(t+1)</sub> + PC1 <sub>(t-1)</sub> + PC3 + PC3 <sub>(t+1)</sub> + PC3 <sub>(t-1)</sub>
<i>P. sylvestris</i>	All	0.19	0.13	0.43	0.9019	0.9019	0.0241	PC1 <sub>(t-1)</sub> + PC3 + PC3 <sub>(t-1)</sub>
	Width	0.19	0.17	0.44	0.8559	0.8559	0.1211	PC1 <sub>(t+1)</sub>
	Anatomy	0.17	0.11	0.41	0.9018	0.9018	0.0242	PC2 <sub>(t+1)</sub> + PC3 + PC3 <sub>(t-1)</sub>

Verification was conducted over the same calibration period using a jackknife approach. The two best models appear in bold

*RMSE* root mean square error, *RE* reduction of error, *SE* standard error of estimate, *r* Spearman correlation coefficient between observed and estimated SPEI

(temperature, precipitation, and SPEI during previous autumn) mainly on ring width variables (TRW, EWW, LWW, and NC) than Scots pine for which the highest correlations were observed between latewood variables (e.g., LWW, CWL, LDL, and LP) and current year summer SPEI. In contrast, summer drought (lower SPEI) the previous year caused Scots pine to produce wider cell walls throughout the entire ring and narrower latewood (Fig. 4).

#### Dendroclimatic models

A total of 18 regression models for the mean SPEI in JA and SO were developed with PCs of different ring variables to test their potential for dendroclimatic reconstructions. Only the first three PCs, with either a  $-1$ -,  $0$ - or  $1$ -year lag, entered the models (Table 3). All models showed some degree of predictive ability with  $R^2$  ranging from 0.17 to 0.45 and a positive reduction of error (RE) in all cases. As expected from results of previous analyses, models that only included *P. nigra* (*P. sylvestris*) variables were weakest for JA SPEI (SO SPEI) (Table 3). The models for mean JA and SO SPEI that included different lags of PC1

and PC3 derived from ring width and anatomy variables from both pine species were the strongest according to calibration and verification statistics (Table 3; Fig. 5).

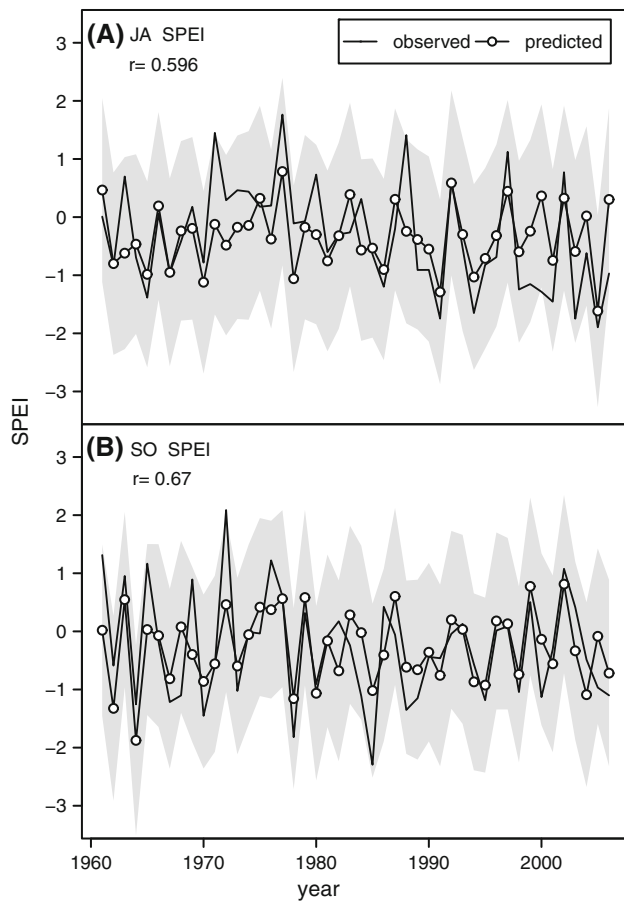
The spatial analysis of correlations between gridded SPEI data and estimated values using the best model for JA and SO showed that the SPEI variability would be well explained by these two models (Fig. 6). Correlations for JA SPEI were highest ( $r > 0.5$ ) in the northern half of Iberia, southern France and northwestern Italy. Results were better for SO SPEI with  $r > 0.5$  in Iberia (including extensive areas with  $r > 0.6$ ), northwestern Italy, northern Morocco, and Algeria (Fig. 6).

## Discussion

### Chronologies

Average radial dimensions for lumen diameter and cell-wall thickness were within the range of those described for other conifers (Panyushkina et al. 2003; Liang et al. 1997; De Micco et al. 2007) although smaller than other

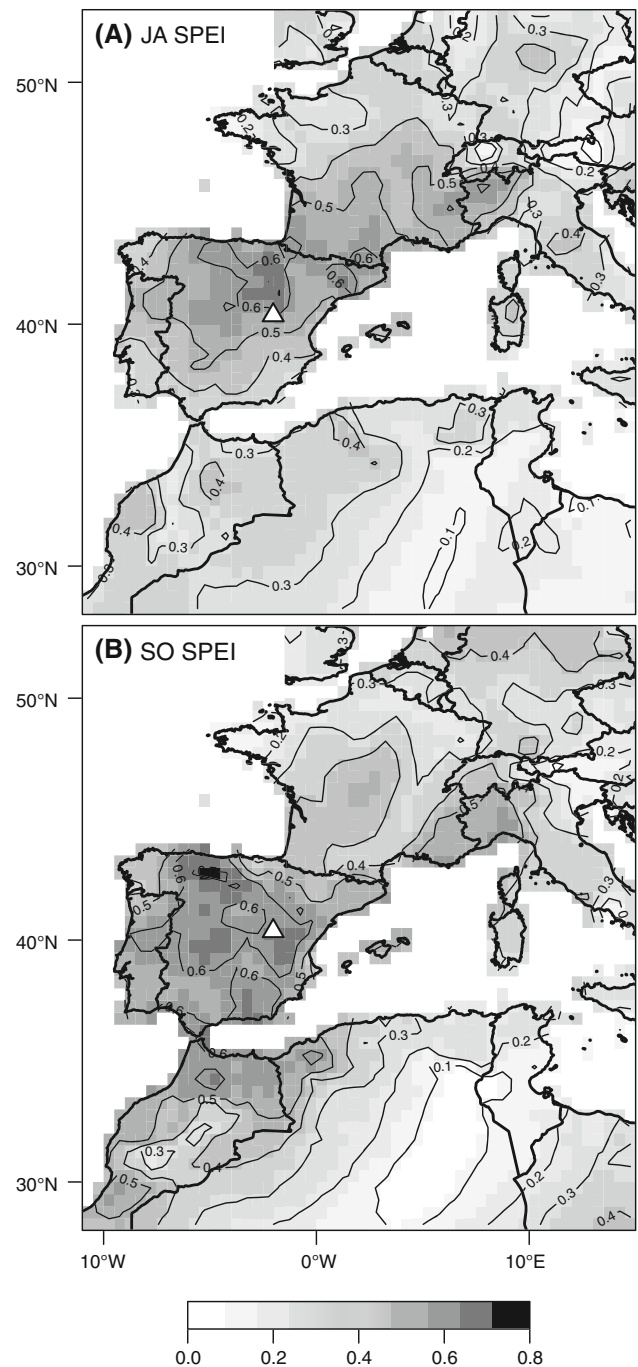




**Fig. 5** Observed and estimated SPEI for the period 1960–2006 using the best two models in Table 3 for **a** July–August (Spearman  $r = 0.596$ ) and **b** September–October (Spearman  $r = 0.670$ ). Gray shade represents the 95 % prediction intervals. Observed SPEI is the mean of the 16 grid points

Mediterranean pines (Attolini et al. 1990). The high positive correlation between ring width and number of cells, also reported for other conifers (Panyushkina et al. 2003; Camarero et al. 1998), indicates that wider rings are the result of greater number of tracheids (cell division) rather than of larger tracheids (cell expansion). The small residual influence of tracheid size on ring width was mainly caused by cell-wall thickness variability and not by lumen diameter, contrary to results found for Scots pine in the Austrian Alps (Gruber et al. 2010). Correlation between latewood percentage and ring width was only significantly positive in *P. nigra*, as previously shown for *Picea mariana* (Mill.) BSP (St-Germain and Krause 2008) and contrary to *Picea abies* (L.) Karst (Wimmer and Grabner 2000). Therefore, wider rings in *P. sylvestris* are characterized by wider earlywood but also by a proportionally wider latewood.

Anatomical chronologies showed in most cases lower common signal and sensitivity than ring width in accordance with results for several ring-porous broadleaved species (e.g., Tardif and Conciatori 2006; Fonti and García-



**Fig. 6** Spatial analysis of Spearman correlations between gridded SPEI data and reconstructed values for the period 1960–2006 using the best two models in Table 3 for **a** July–August (maximum  $r = 0.71$ ) and **b** September–October (maximum  $r = 0.73$ )

Gonzalez 2004). This is most probably caused by the narrower variability range of tracheid sizes than those of ring widths, which also includes the higher variability in the number of tracheids (Table 1). Tracheid time series were also characterized by lower autocorrelation as they respond to environmental factors at their time of formation (e.g., Deslauriers and Morin 2005; Attolini et al. 1990;

Gindl et al. 2000; Donaldson 2002). The higher autocorrelation of cell-wall width in the earlywood is caused by its dependency on stored carbohydrates from the previous year while latewood growth (wall width) relies on current photoassimilates (Hoch et al. 2003).

#### Relationship between chronologies and monthly climate variables

In general, the effect of temperatures on radial growth during the current year was opposite to that of precipitation. This interaction between temperature and precipitation, which is summarized in the drought index SPEI, caused tree growth (either width or anatomical variables) to show the highest correlations with SPEI. Previous autumn precipitation (temperature) had a positive (negative) effect on growth the following year as a result of their influence on carbohydrates accumulation and cambial zone formation (Vaganov et al. 2006; Hoch et al. 2003). Higher winter temperatures enhanced growth reflecting the temperature limitation of photosynthesis during the cold season and the importance of fixed carbon before the growing season (Hoch et al. 2003). In late winter or early spring, warmer temperatures also cause cambium activation (Gricar et al. 2006; Rossi et al. 2008) and earlier bud burst (Rötzer et al. 2004).

The transition from earlywood to latewood formation is considered to be affected by photoperiod (Rossi et al. 2006) through hormonal control (Uggla et al. 2001). In our study site, drought affects latewood development more than earlywood because water availability becomes limiting in late spring-early summer. Higher water availability after the summer solstice would allow pines to extend the period of latewood production (wider latewood, higher latewood percentage, and thicker cell walls in latewood) rather than producing wider earlywood by postponing the onset of latewood development (Wimmer and Grabner 2000). Periods of drought or high temperatures have several effects on tree physiology and growth. In drier conditions, cambial activity stops earlier (Pichler and Oberhuber 2007) causing consistently shorter periods of wood formation (Gruber et al. 2010). The higher evaporative demand or lower water availability causes stomata to close reducing plant gas exchange and carbon uptake (Jones 1998). In addition, under drought stress, trees might allocate more carbon to reserves (Wiley and Helliker 2012), favor root development (Dewar et al. 1994), and in general have lower cambial activity reducing cambial division and cell-wall thickening (Cinnirella et al. 2002; Irvine et al. 1998; Piovesan et al. 2008). However, according to our results and those by Eilmann et al. (2009), drought did not reduce cell lumen expansion in Scots pine as it responded by producing fewer latewood tracheids with a wider lumen

and thinner cell wall. Wider tracheid lumens have also been observed in desert versus montane *Pinus ponderosa* (Maherali and DeLucia 2000). Black pine had a similar but weaker response to current drought, and it was more influenced by previous-year climate. Wider lumen conduits provide higher hydraulic efficiency at a lower carbon cost (Tyree and Zimmermann 2002; Maherali and DeLucia 2000), although they might be more vulnerable to cavitation especially if they also have thinner cell walls (Hacke and Sperry 2001). The stronger negative effect of drought on wall thickening of tracheids in Scots pine reduces their cavitation resistance. Although we observed no significant mortality of black pine or Scots pine in the study area, higher levels of drought-induced embolism in Scots pine have been linked to increased mortality observed in NE Spain (Martínez-Vilalta and Piñol 2002).

#### Dendroclimatic potential of tracheid time series

Anatomical variables in our study added advantages toward understanding the mechanisms and timing of the climate influences by emphasizing correlations that otherwise would have gone unnoticed, similar to findings of previous studies in conifers (De Grandpré et al. 2011). Some of the anatomical chronologies display common signal (EPS and Rbar) almost as high as those of ring width variables had lower AC and cell-wall thickness appears to change little with tree age (Panyushkina et al. 2003). Some of them (e.g., cell-wall thickness, number of cells or percentage of latewood) showed stronger correlations with climate, particularly SPEI, than did ring width variables in accordance with the few studies that have analyzed the climate signal recorded in tracheid time series (Panyushkina et al. 2003; Wang et al. 2002; Yasue et al. 2000). Our results indicated that summer as well as late summer to early autumn drought conditions (mean July–August and September–October SPEI) would be better reconstructed by including width and anatomical variables as proxies. A closer analysis by species showed that Scots pine ring variables were strong predictors of JA drought while black pine was a better predictor for SO conditions. Combining variables of both species with different temporal response to water availability through PCR modeling significantly improves their reconstruction ability. These models showed a good behavior at broad geographical scales suggesting that our ring variable chronologies are reflecting not only the product of a local response but rather general atmospheric conditions as well. During July and August (JA), tree-ring features showed a greater spatial correlation with SPEI for the highlands of north-central Spain, the Ligurian Sea area (southern France and northwestern Italy) and several discontinuous mountain areas of northern Africa. This pattern is in accordance with the greater

influence of cyclonic activity and thermal lows on precipitation in the western Mediterranean during summer (Trigo et al. 1999), suggesting a Mediterranean source of moisture at our tree-ring site. In September and October, we found greater correlation with northwestern Spain, western France, and Morocco where autumn precipitation is associated with westerly flow coinciding with the weakening of the Azores high (Esteban-Parra et al. 1998).

These results support previous observations suggesting that paleoclimate or streamflow reconstructions can be improved by using tree rings from multiple species (Maxwell et al. 2011; Cook and Pederson 2010) or multiple ring proxies (McCarroll et al. 2003; Hughes et al. 1994). However, our two single most important anatomical proxies for drought, that is, total number of cells and latewood cell-wall thickness, are highly correlated with tree-ring width (Table 3; Camarero et al. 1998) and maximum density (Wang et al. 2002; Yasue et al. 2000), respectively, which probably suggests that ring width and density would have been similarly accurate proxies. Maximum ring density explains more variance than any anatomical variables (Wang et al. 2002; Wimmer and Grabner 2000), and it might be a better and more stable proxy than ring width for summer temperatures at cold limited sites (Andreu-Hayles et al. 2011) and drought at arid sites (Hughes et al. 1994).

## Conclusion

Our results suggest that more complete climate-growth relationships (i.e., several periods of the year and for broader spatial scales) can be obtained by developing time series of different tree-ring features and different species that could allow to use tree rings of Scots pine and black pine from more mesic sites. These relationships might prove useful for dendroclimatic reconstructions. However, the limited time span of our chronologies does not allow for more conclusive results, and further analysis with longer periods and broader spatial scale might be needed. In addition, measurements of maximum density are easier and less time consuming than anatomical features and could be preferred for dendroclimatology. Nonetheless, anatomical variables can provide different information at higher time resolutions than the most widely used ring width variables (Fonti et al. 2010; Wang et al. 2002). They might also allow extracting climatic information from trees not growing at extreme habitats (i.e., cold or drought limited) but at temperate ones, which might have recorded a mixed temperature-precipitation signal. Wood anatomical variables also add very important ecological information on tree physiology, growth, and climate effects upon it (Eckstein 2004; Fonti et al. 2010). Especially interesting in

this sense might be the investigation of the hydraulic adjustment of trees' xylem to climatic conditions regarding their adaptation to climate change, competition, and survival (Eilmann et al. 2009; Gea-Izquierdo et al. 2012).

**Acknowledgments** The authors wish to thank Nele Schmitz for her help and advice on wood sample preparation. Caroline Leland provided critical feedback that improved an earlier version of this manuscript. The Spanish National Meteorological Agency (AEMET) provided climate data. Two anonymous reviewers provided suggestions that helped improve an earlier version of this manuscript. Lamont-Doherty Earth Observatory Contribution No. 7598. This work has been supported by the Spanish Ministry of Science of Education through project AGL2010.21153.02.01. D. M-B was supported by a Fulbright-MICIIN postdoctoral fellowship.

## References

- Akaike H (1974) A new look at the statistical model identification. *IEEE Trans Autom Control* 19(6):716–723
- Andreu L, Gutierrez E, Macias M, Ribas M, Bosch O, Camarero JJ (2007) Climate increases regional tree-growth variability in Iberian pine forests. *Glob Change Biol* 13:1–12
- Andreu-Hayles L, Rosanne DA, Anchukaitis KJ, Beck PSA, Frank D, Goetz S (2011) Varying boreal forest response to Arctic environmental change at the Firth River, Alaska. *Env Res Let* 6(4):045503
- Assmann E (1970) The principles of forest yield study. Pergamon Press Ltd., Oxford
- Attolini MR, Calvani F, Galli M, Nanni T, Ruggiero L, Schaer E, Zuanni F (1990) The relationship between climate variables and wood structure in *Pinus halepensis* Mill. *Theor Appl Climatol* 41:121–127
- Barbéro M, Losiel R, Queézel P, Richardson DM, Romane F (1998) Pines of the mediterranean basin. In: Richardson DM (ed) *Ecology and biogeography of pinus*. Cambridge University Press, Cambridge
- Beeckman H, Van der Mijnsbrugge K (1993) Redundancy analysis and the evolutionary learning algorithm as complementary mathematical processing tools for dendrochronological data sets. *Silva Gandavensis* 58:101–113
- Brodribb T, Hill RS (1999) The importance of xylem constraints in the distribution of conifer species. *New Phytol* 143(2):365–372
- Bunn AG (2008) A dendrochronology program library in R (dplR). *Dendrochronologia* 26(2):115–124
- Camarero JJ, Guerrero-Campo J, Gutiérrez E (1998) Tree ring growth and structure of *Pinus uncinata* and *Pinus sylvestris* in the central Spanish Pyrenees. *Arct Alp Res* 30(1):1–10
- Campelo F, Nabais C, Gutiérrez E, Freitas H, García-González I (2010) Vessel features of *Quercus ilex* L. growing under Mediterranean climate have a better climatic signal than tree-ring width. *Trees* 24(3):463–470
- Cherubini P, Gartner BL, Tognetti R, Bräker OU, Schoch W, Innes JL (2003) Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. *Biol Rev* 78:119–148
- Cinnirella S, Magnani F, Saracino A, Borghetti M (2002) Response of a mature *Pinus laricio* plantation to a three-year restriction of water supply: structural and functional acclimation to drought. *Tree Physiol* 22:21–30
- Cook ER, Pederson N (2010) Uncertainty, emergence, and statistics in dendrochronology. In: Hughes MK, Swetnam TW, Diaz HF

- (eds) Dendroclimatology: progress and prospects, developments in paleoecological research. Springer, Berlin
- Cook ER, Meko DM, Stahle DW, Cleaveland MK (1999) Drought reconstructions for the continental United States. *J Clim* 12:1145–1162
- Cook ER, Esper J, D'Arrigo RD (2004) Extra-tropical Northern Hemisphere land temperature variability over the past 1000 years. *Quat Sci Rev* 23(20–22):2063–2074
- Cook ER, Anchukaitis KJ, Buckley BM, D'Arrigo RD, Jacoby GC, Wright WE (2010) Asian monsoon failure and mega drought during the last millennium. *Science* 328(5977):486–489
- D'Arrigo R, Wilson R, Jacoby G (2006) On the long-term context for late twentieth century warming. *J Geophys Res* 111(D3):D03103
- De Grandpré L, Tardif JC, Hessler A, Pederson N, Conciatori F, Green TR, Oyunsanaa B, Baatarbileg N (2011) Seasonal shift in the climate responses of *Pinus sibirica*, *Pinus sylvestris*, and *Larix sibirica* trees from semi-arid, north-central Mongolia. *Can J For Res* 41(6):1242–1255
- De Micco V, Saurer M, Aronne G, Tognetti R, Cherubini P (2007) Variations of wood anatomy and  $\delta^{13}\text{C}$  within-tree rings of coastal *Pinus pinaster* showing intra-annual density fluctuations. *IAWA J* 28(1):61–74
- Deslauriers A, Morin H (2005) Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. *Trees* 19(4):402–408
- Dewar RC, Ludlow AR, Dougherty PM (1994) Environmental influences on carbon allocation in pines. *Ecol Bull* 43:92–101
- Donaldson LA (2002) Abnormal lignin distribution in wood from severely drought stressed *Pinus radiata* trees. *IAWA J* 23(2):161–178
- Eckstein D (2004) Change in past environments—secrets of the tree hydrosystem. *New Phytol* 163:1–4
- Eilmann B, Zweifel R, Buchmann N, Fonti P, Rigling A (2009) Drought-induced adaptation of the xylem in Scots pine and pubescent oak. *Tree Physiol* 29:1011–1020
- Esper J, Cook ER, Schweingruber FH (2002) Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science* 295(5563):2250–2253
- Esteban-Parra MJ, Rodrigo FS, Castro-Diez Y (1998) Spatial and temporal patterns of precipitation in Spain for the period 1880–1992. *Int J Climatol* 18:1557–1574
- Filion L, Courmoyer L (1995) Variation in wood structure of eastern larch defoliated by the larch sawfly in subarctic Quebec. *Can J For Res* 25(8):1263–1268
- Fonti P, García-González I (2004) Suitability of chestnut earlywood vessel chronologies for ecological studies. *New Phytol* 163:77–86
- Fonti P, von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *New Phytol* 185(1):42–53
- Gea-Izquierdo G, Cherubini P, Cañellas I (2011) Tree-rings reflect the impact of climate change on *Quercus ilex* L. along a temperature gradient in Spain over the last 100 years. *For Ecol Manag* 262(9):1807–1816
- Gea-Izquierdo G, Fonti P, Cherubini P, Martín-Benito D, Chara H, Cañellas I (2012) Xylem hydraulic adjustment and growth response of *Quercus canariensis* wild to climatic variability. *Tree Physiol* 32(4):401–413
- Gindl W, Grabner M, Wimmer R (2000) The influence of temperature on latewood lignin content in treeline Norway spruce compared with maximum density and ring width. *Trees* 14:409–414
- Gricar J, Zupancic M, Cufar K, Koch G, Schmitt UWE, Oven P (2006) Effect of local heating and cooling on cambial activity and cell differentiation in the stem of Norway spruce (*Picea abies*). *Ann Bot* 97(6):943–951
- Gruber A, Strobl S, Veit B, Oberhuber W (2010) Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. *Tree Physiol* 30(4):490–501
- Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. *Perspect Plant Ecol Evol Syst* 4(2):97–115
- Hoch G, Richter A, Körner C (2003) Non-structural carbon compounds in temperate forest trees. *Plant, Cell Environ* 26(7):1067–1081
- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull* 43:69–78
- Hughes MK (2002) Dendrochronology in climatology—the state of the art. *Dendrochronologia* 20(1–2):95–116
- Hughes MK, Xiangding W, Xuemei S, Garfin GM (1994) A preliminary reconstruction of rainfall in north-central China since A.D. 1600 from tree-ring density and width. *Quatern Res* 42(1):88–99
- Irvine J, Perks MP, Magnani F, Grace J (1998) The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiol* 18:393–402
- Jones H (1998) Stomatal control of photosynthesis and transpiration. *J Exp Bot* 49:387–398
- Kirdyanov A, Hughes M, Vaganov E, Schweingruber F, Silkin P (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees* 17(1):61–69
- Körner C (2003) Carbon limitation in trees. *J Ecol* 91(1):4–17
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier Science BV, Amsterdam
- Liang C, Filion L, Courmoyer L (1997) Wood structure of biotically and climatically induced light rings in eastern larch (*Larix laricina*). *Can J For Res* 27:1538–1547
- Maherali H, DeLucia EH (2000) Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiol* 20:859–867
- Martín-Benito D, del Río M, Cañellas I (2010) Black pine (*Pinus nigra* Arn.) growth divergence along a latitudinal gradient in Western Mediterranean mountains. *Ann For Sci* 67(4):401
- Martínez-Vilalta J, Piñol J (2002) Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For Ecol Manag* 161(1–3):247–256
- Maxwell RS, Hessler AE, Cook ER, Pederson N (2011) A multispecies tree ring reconstruction of Potomac River stream flow (950–2001). *Water Resour Res* 47(5):W05512
- McCarroll D, Jalkanen R, Hicks S, Tuovinen M, Gagen M, Pawellek F, Eckstein D, Schmitt U, Autio J, Heikkinen O (2003) Multiproxy dendroclimatology: a pilot study in northern Finland. *The Holocene* 13(6):829–838
- Meehl GA, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305(5686):994–997
- Navarro Cerrillo RM, Varo MA, Lanjeri S, Hernández Clemente R (2007) Cartografía de defoliación en los pinares de pino silvestre (*Pinus sylvestris* L.) y pino salgareño (*Pinus nigra* Arnold.) en la Sierra de los Filabres. *Ecosistemas* 16(3):163–171
- Nicault A, Alleaume S, Brewer S, Carrer M, Nola P, Guiot J (2008) Mediterranean drought fluctuation during the last 500 years based on tree-ring data. *Clim Dynam* 31(2):227–245
- Nikolov N, Helmsaari H (1992) Silvics of the circumpolar boreal forest tree species. In: Shugart HH, Leemans R, Bonan GB (eds) A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, pp 13–84
- Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H (2008) Vegan: community ecology package. R package version 1.15-0. <http://cran.r-project.org/>, <http://vegan.r-forge.r-project.org/>
- Panyushkina IP, Hughes MK, Vaganov EA, Munro MAR (2003) Summer temperature in northeastern Siberia since 1642 reconstructed from

- tracheid dimensions and cell numbers of *Larix cajanderi*. *Can J For Res* 33:1905–1914
- Pichler P, Oberhuber W (2007) Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *For Ecol Manag* 242:688–699
- Piovesan G, Biondi F, Di Filippo A, Alessandrini A, Maugeri M (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica*) forests of the central Apennines, Italy. *Glob Change Biol* 14:1265–1281
- Pittermann J, Sperry JS, Wheeler JK, Hacke UG, Sikkema EH (2006) Mechanical reinforcement of tracheids compromises the hydraulic efficiency of conifer xylem. *Plant, Cell Environ* 29:1618–1628
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Rasband WS (1997) ImageJ (1.38x). U.S. National Institutes of Health, Bethesda, Maryland, USA
- Rossi S, Deslauriers A, Anfodillo T, Morin H, Saracino A, Motta R, Borghetti M (2006) Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytol* 170(2):301–310
- Rossi S, Deslauriers A, Gričar J, Seo J-W, Rathgeber CB, Anfodillo T, Morin H, Levanic T, Oven P, Jalkanen R (2008) Critical temperatures for xylogenesis in conifers of cold climates. *Glob Ecol Biogeogr* 17(6):696–707
- Rötzer T, Grote R, Pretzsch (2004) The timing of bud burst and its effect on tree growth. *Int J Biometeorol* 48:109–118
- Schmitz N, Verheyden A, Kairo JG, Beeckman H, Koedam N (2007) Successive cambia development in *Avicennia marina* (Forssk.) Vierh. is not climatically driven in the seasonal climate at Gazi Bay, Kenya. *Dendrochronologia* 25:87–96
- St-Germain J-L, Krause C (2008) Latitudinal variation in tree-ring and wood cell characteristics of *Picea mariana* across the continuous boreal forest in Quebec. *Can J For Res* 38(6):397–1405
- Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. University of Chicago Press, Chicago
- Tardif J, Conciatori F (2006) Influence of climate on tree rings and vessel features in red oak and white oak growing near their northern distribution limit, Southwestern Quebec, Canada. *Can J For Res* 36:2317–2330
- Ter Braak CJF (1994) Canonical community ordination. Part I: basic theory and linear methods. *Ecoscience* 1(2):127–140
- Trigo IF, Davies TD, Bigg GR (1999) Objective climatology of cyclones in the mediterranean region. *J Clim* 12(6):1685–1696
- Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap. Springer Verlag, New York
- Uggla C, Magel E, Moritz T, Sundberg B (2001) Function and dynamics of auxin and carbohydrates during earlywood/latewood transition in scots pine. *Plant Physiol* 125:2029–2039
- Vaganov EA, Hughes MK, Shaskin AV (2006) Growth dynamics of conifer tree rings—images of past and futures environments. Springer, Heidelberg
- Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J Clim* 23(7):1696–1718
- Vysotskaya LG, Vaganov EA (1989) Components of the variability of radial cell size in tree rings of conifers. *IAWA Bulletin* 10:417–428
- Wang L, Payette S, Bégin Y (2002) Relationships between anatomical and densitometric characteristics of black spruce and summer temperature at tree line in northern Quebec. *Can J For Res* 32(3):477–486
- Wiley E, Helliker B (2012) A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New Phytol* 195(2):285–289
- Wimmer R, Grabner M (2000) A comparison of tree-ring features in *Picea abies* as correlated with climate. *IAWA J* 21(4):403–416
- Yasue K, Funada R, Kobayashi O, Ohtani J (2000) The effects of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climatic factors. *Trees* 14:223–229