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ORIGINAL PAPER

Climatic signals in tree-ring widths and wood structure of *Pinus halepensis* in contrasted environmental conditions

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Abstract Tree-ring widths (RW), earlywood (EW) and latewood (LW) widths, the transition from early to latewood (*T*) and the occurrence of intra-annual density fluctuations in EW (E-ring) and in LW (L-ring), as well as the presence of resin canals in EW and LW, were analyzed in Aleppo pine (*Pinus halepensis* Mill.) from three sites in Spain and one in Slovenia to find out if the anatomical characteristics can provide additional seasonal climate–growth information from contrasted environmental conditions. Principal component analysis was applied to elucidate the relationship between the measured parameters and climate. Principal component factor PC1 proved to be related to parameters of EW and the climatic variables of winter-spring; PC2 to parameters of LW and climatic variables of summer–autumn; PC3 to conditions during transitions from humid to dry periods. The three PCs vary between sites and are determined by the climatic conditions during their formation. The study demonstrates that wood anatomical features may provide complementary information to that contained in tree-ring widths. Since such results are obtained on contrasting sites, it is likely that it may be generalized over the wide range of *P. halepensis* distribution representing a useful proxy for studies on a regional scale.

Keywords *Pinus halepensis* · Mediterranean · Tree rings · Intra-annual density fluctuations · Anatomical characteristics

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Introduction

The study of wood anatomical features in tree rings represents a promising approach in the research of tree biology and climate change (Fonti et al. 2010), allowing a detailed analysis of climate events within the growing season (Campelo et al. 2007; Olivar et al. 2012). It facilitates the determination of how climate variability and change may modify growth rates and wood structure which are crucial for hydraulic and mechanical performance of wood (Froux et al. 2002; de Micco et al. 2008; Martinez-Meier et al. 2008; Hoffmann et al. 2011).

Tree rings contain several wood anatomical elements that can be quantified, and it has been shown that, for instance, earlywood and latewood widths can provide more detailed information than the total tree-ring widths (Lebourgeois et al. 2010). Other anatomical characteristics, such as the occurrence of intra-annual density fluctuations (IADFs) and the presence of resin canals have also proven to be highly dependent on climatic variability (Wimmer and Grabner 1997; Rigling et al. 2003; Cherubini et al. 2003; Campelo et al. 2007; Bogino and Bravo 2009; Vieira et al. 2009; Battipaglia et al. 2010; Fonti et al. 2010).

The combination of ring-width variables and wood anatomical features can help better interpret growth–climate relations and the physiological processes behind them, than can the use of tree-ring widths alone. This combination can be used as a climate multiproxy and to improve the predictions of the potential impact of climate change on tree growth and survival (Wimmer and Grabner 1997; Wimmer et al. 2000; McCarroll et al. 2003; Rathgeber et al. 2005; Battipaglia et al. 2010; Campelo et al. 2010; de Luis et al. 2011a).

However, it is still not well understood whether the information on seasonal climatic influences derived from different anatomical characteristics is redundant or complementary to that obtained from the tree-ring widths. In addition, such analyses over the full range of distribution would allow comparisons of how the same species operate across different environmental conditions.

Aleppo pine (*Pinus halepensis* Mill.) is the most widespread pine species in the Mediterranean and can grow under widely diverse climatic conditions (Barbéro et al. 1998; Richardson and Rundel 1998). Because of this, it is very appropriate for the studies across the Mediterranean, where the climate ranges from nearly desert to temperate regimes.

Pinus halepensis has typical conifer wood structure, containing resin canals and clearly distinguishable earlywood and latewood, with a gradual transition between them (Schweingruber 1988). Due to the high variability of intra-annual patterns of cambial activity in the Mediterranean area, wood anatomical features often differ from the normal patterns (Cherubini et al. 2003). Recent studies in this species have shown that missing tree rings (Novak et al. 2011), IADFs (de Luis et al. 2011a; Olivar et al. 2012), and the presence or absence of tangential bands of resin canals (de Luis et al. 2007) are related to the climatic conditions during the wood formation. However, since wood-formation studies are relatively rare, and as a rule limited to one or few seasons, how they could complement the long-term information obtained from tree-ring widths is still not well investigated.

The purpose of the present study was to record structural features in wood of *P. halepensis* and to evaluate the influence of seasonal climatic conditions on it, using combined information of tree-ring widths and their anatomical characteristics. The study was conducted on four different sites across the distribution range of *P. halepensis*, with the aims (1) to evaluate if the effect of climatic factors can be generalized under contrasted environmental conditions, (2) to better interpret climate–growth relationship on seasonal scale, and (3) to determine if the information contained in tree rings can be valuable as a proxy for the regional studies.

Materials and methods

Study site and climatic conditions

The study was carried out in four Mediterranean sites with contrasting climate conditions for *P. halepensis*. Three sites are located in Spain and one in Slovenia (Fig. 1).

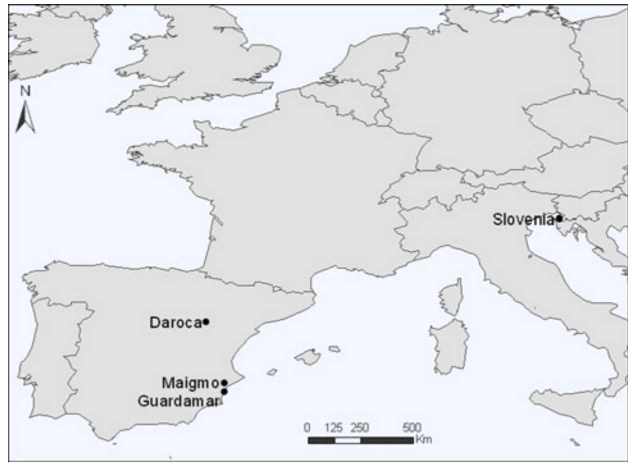

Fig. 1 Four sampling sites: Guardamar (Lat. 38.11°, Long. −0.64°, 5 m asl), Maigmo (Lat. 38.50°, Long. −0.64°, 844 m asl), Daroca (Lat. 41.11°, Long. −1.41°, 800 m asl), and Slovenia (Lat. 45.50°, Long. 13.70°, 80 m asl)

For the period 1950–2000, Guardamar (Lat. 38.11°, Long. −0.64°, 5 m asl) is characterized by a dry and warm climate (276.4 mm, 17.7 °C) and represents one of the southern distribution limits of *P. halepensis* in Europe. Maigmo (Lat. 38.50°, Long. −0.64°, 844 m asl) is located close to Guardamar, but in the inland mountain area, with more precipitation (369.3 mm, 13.9 °C). Daroca (Lat. 41.11°, Long. −1.41°, 900 m asl) is located inland in the Iberian Peninsula and has a Mediterranean continental climate (428.6 mm, 12.4 °C). The fourth site is located in the coastal area of Slovenia, in the place named Krkavce (Lat. 45.45°, Long. 13.68°, 40 m asl), where the annual amount precipitation is 1,027.4 mm, and mean annual temperature is 14.3 °C, and represents the northern distribution limit of *P. halepensis* in Europe. Climate diagrams of monthly mean climate conditions for the four sites studied are shown in Fig. 2.

Sampling strategy

Sampling was conducted on mature, apparently healthy trees of *P. halepensis*, without any visible damage, with a range of inside dates of 1912–2000 for Guardamar, of 1868–2000 for Maigmo, of 1934–2006 for Daroca, and of 1920–2004 for Slovenia. We selected 15 trees per site, and extracted two cores at the breast height from each. The cores were then labeled, fixed on wooden supports, air-dried and sanded with progressively finer grades of sandpaper (80, 180, 300, 500 grit) until the tree-ring structure was clearly visible under the stereo microscope.

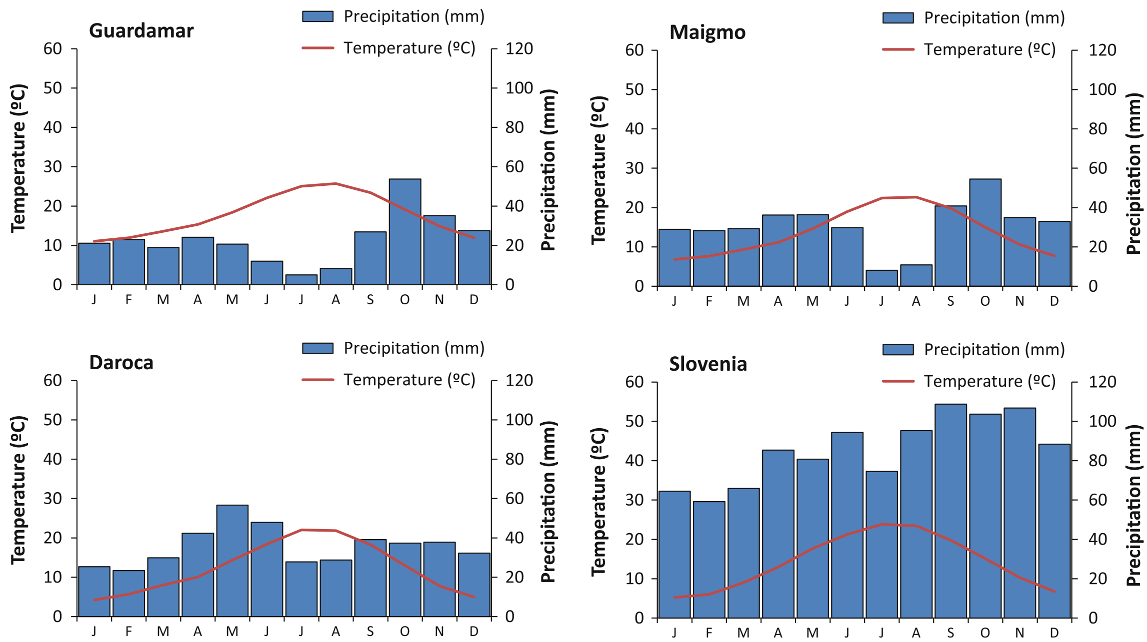

Fig. 2 Long-term (1950–2000) climate conditions at four sites studied: Guardamar, Maigmo, Daroca and the coastal area of Slovenia. *Blue bars* are total monthly precipitations in mm and the *red line* is the average annual temperature in °C

Tree-ring measurements

The earlywood (EW) width, latewood (LW) width and total tree-ring (RW) width of each annual tree ring were measured under a stereo microscope with an accuracy of 0.01 mm, with the TSAP-Win program and LINTAB™ 5 measuring device (Rinntech®, Heidelberg, Germany, www.rinntech.com).

The tree-ring series were visually and statistically cross-dated and compared between each other by calculating the *t* value after Baillie and Pilcher (1973) using TSAP/X and TSAP-Win. Additionally the quality of cross-dating was verified using the program COFECHA (Holmes 1994).

The individual RW, EW and LW width series were standardized using the ARSTAN program (Cook and Holmes 1986) by removing long-term trends using a negative exponential function followed by a cubic smoothing spline with a 50 % cutoff frequency and a response period of 30 years. The autocorrelation filter was then applied to the de-trended series to remove correlations between consecutive measurements and to obtain residual series containing only the high-frequency variations in year-to-year growth series, expected to be mainly related to year-to-year climatic variability. Thereafter, a bi-weight robust estimation of the mean was applied to construct residual chronologies (Cook and Peters 1997). An expressed population signal (EPS) of 0.85 was used as a threshold to determine the usable length of each indexed chronology for the subsequent analysis (Wigley et al. 1984).

Anatomical characterization of tree rings

For the same series, and the same period 1950–2000, we next analyzed the anatomical characteristics of tree rings (Fig. 3), i.e., (1) the presence of latewood-like cells within the earlywood (E-ring), (2) the presence of earlywood-like cells within the latewood (L-ring), (3) the presence of resin canals in earlywood (RC–EW), (4) the presence of resin canals in latewood (RC–LW), and (5) whether the transition between EW and LW in the ring (*T*) was gradual or abrupt (Fig. 4). For E-ring, L-ring, RC–EW and RC–LW, we assigned the value 1 if the characteristics were present in the dated tree ring, and the value 0 if it was absent. In the case of *T*, we assigned the value 1 if transition was abrupt, and 0 if it was gradual.

The frequency of each characteristic per year (*F*), at each site was calculated as the ratio:

$$F = N/n$$

where *N* is the number of tree rings in which the given anatomical characteristics were present, and *n* is the total number of tree rings analyzed. Changing the number of tree rings (*n*) over time may generate a bias in the variance of the frequency series. To address this problem, the adjustment proposed by Osborn et al. (1997) was used to stabilize the variance. Next, we calculated stabilized frequency (*f*), according to:

$$f = F\,n^{0.5}$$

Finally, a negative exponential function followed by a cubic smoothing spline with a 50 % cutoff frequency and

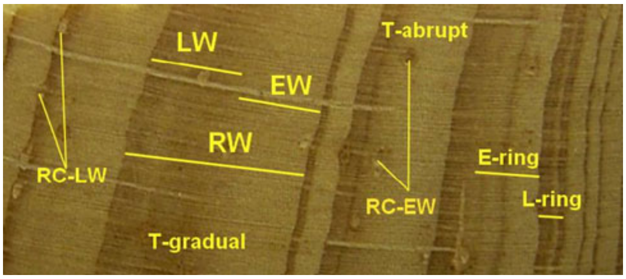

Fig. 3 Tree rings of *P. halepensis* and their anatomical characteristics: tree ring (RW), earlywood (EW), and latewood (LW) widths, E-ring (latewood-like cells in earlywood), L-ring (earlywood-like cells in latewood), RC–EW (resin canals in earlywood), RC–LW (resin canals in latewood), transition between earlywood and latewood (*T* abrupt) and (*T* gradual)

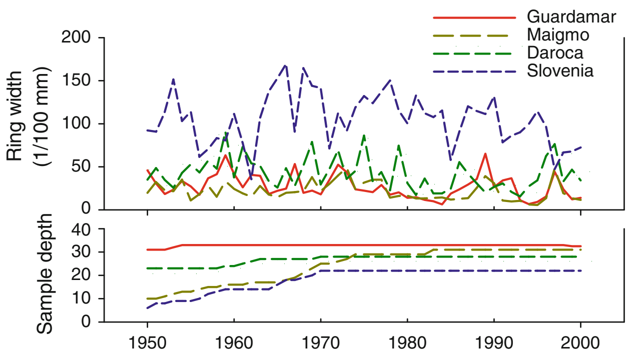

Fig. 4 Mean ring-width chronologies and sample depth at four sites studied

a response period of 30 years were applied to the stabilized frequency (*f*) to remove long-term trend and autocorrelation, and obtain a residual series of *f*.

Dendroclimatological analysis

The residual chronologies and residual series of tree-ring anatomical characteristics (*f*) were normalized to a mean of zero and the standard deviation of one. Then, principal component analysis (PCA) of the covariance matrix of RW, EW and LW normalized residual series and E-ring, L-ring, RC–EW, RC–LW and *T* normalized residual series was used for grouping the characteristics with similar year-to-year variations. These components were rotated orthogonally according to the Varimax criterion. The most representative principal components were selected according to Kaiser's rule (eigenvalue > 1) (Kaiser 1992) and the weighting components (rotated component loadings) were examined to identify the pattern of association of RW, EW, LW, E-ring, L-ring, RC–EW, RC–LW and *T* with each component.

The climatic signal was investigated by correlating the significant PCA eigenvectors with climatic factors obtained from four different Mediterranean sites using the program DendroClim2002 (Biondi and Waikul 2004). The correlation function analysis was made using the significant principal component eigenvectors (PC1, PC2 and PC3) as dependent variables, while the independent variables were the monthly mean temperatures and the monthly sums of precipitation for each year from September of the previous year to December of the current year.

We obtained climatic data from the meteorological stations close to each sampling site from the Meteorological Agency of Spain and Environmental Agency of the Republic of Slovenia (ARSO). The analysis focused on a common period from 1950 to 2000 according to the availability of high-quality meteorological data and well-replicated chronologies.

Results

Tree-ring chronologies and anatomical characteristics

For the period 1950–2000, the largest mean widths of RW, EW and LW are found in Slovenia, followed by Daroca, then Maigmo and the smallest are in Guardamar (Fig. 4; Table 1). Mean frequencies of different anatomical characteristics vary in different places (Table 1; Fig. 4). The frequency of E-rings is the highest in Slovenia and lowest in Maigmo. The frequency of L-rings is highest in Guardamar and they were not found in Slovenia. Resin canals are more common in EW than in LW in all sites. The frequency of RC–EW ranges from the highest in Slovenia, followed by Daroca, then Maigmo, to the lowest in Guardamar. The frequency of RC–LW is the highest in Maigmo and lowest in Guardamar. Maigmo has the highest frequency of gradual transition between EW and LW, whereas it is the least gradual (i.e., the most abrupt) in Slovenia.

Mean sensitivity (MS) of residual RW, EW, LW and anatomical characteristics series (Table 2) varied in Guardamar between 0.282 and 0.697, in Maigmo between 0.071 and 0.554, in Daroca between 0.414 and 0.972, and in Slovenia between 0.216 and 0.649.

Common and uncommon variability in tree-ring characteristics

Year-to-year variations of tree-ring widths and their anatomical characteristics can be summarized in each site by three different uncorrelated time series, PC1, PC2 and PC3 (Fig. 5a–d). PC1 accounted for between 34.9 and 38.3 %, PC2 between 21.0 and 25.8 % and PC3 between 12.1 and 15.5 % of the total variance (Table 3).

Table 1 Mean widths (mm) of tree rings (RW), earlywood (EW) and latewood (LW), and mean frequencies (%) of anatomical characteristics: E-ring (latewood-like cells in earlywood), L-ring (earlywood-like cells in latewood), RC–EW (resin canals in earlywood), RC–LW (resin canals in latewood), *T* (transition between earlywood and latewood where $T = 100$ % is abrupt and $T = 0$ % is gradual) at four sites for the period 1950–2000

	RW (mm)	EW (mm)	LW (mm)	E-ring (%)	L-ring (%)	RC–EW (%)	RC–LW (%)	*T* (%)
Guardamar	0.87	0.60	0.27	2.3	14.5	21.4	5.5	49.0
Maigmo	0.99	0.78	0.22	0.4	3.2	26.4	15.6	72.1
Daroca	1.95	1.53	0.42	5.6	11.1	47.1	10.4	58.3
Slovenia	3.73	2.68	1.05	9.4	0.0	60.5	13.3	34.4

Table 2 Mean sensitivity (MS) of residual series for tree-ring (RW) widths, earlywood (EW) and latewood (LW) widths and their anatomical characteristics: E-ring (latewood-like cells in earlywood), L-ring (earlywood-like cells in latewood), RC–EW (resin canals in earlywood), RC–LW (resin canals in latewood), *T* (transition from earlywood to latewood) at four sites for the period 1950–2000

	RW	EW	LW	E-ring	L-ring	RC–EW	RC–LW	*T*
Guardamar	0.316	0.365	0.282	0.306	0.679	0.506	0.660	0.423
Maigmo	0.405	0.458	0.432	0.071	0.554	0.416	0.529	0.217
Daroca	0.421	0.453	0.429	0.693	0.972	0.465	0.939	0.414
Slovenia	0.229	0.220	0.271	0.649	0.000	0.216	0.595	0.506

PC1 (Fig. 6a) in all sites describes year-to-year variation of EW and total RW. The frequency of RC–EW is also positively related to PC1 indicating that, if EW is wider, there is a higher probability of RC–EW.

On the other hand, PC2 (Fig. 6b) is positively related to year-to-year variations in LW and the frequency of L-rings. Furthermore, in Slovenia, transition from EW and LW is not related to PC1 (as in the Spanish sites) but rather to LW (PC2), indicating that gradual transition from EW to LW mainly occurs in tree rings with wide LW (negative correlation between PC2 and the frequency of abrupt transition).

Year-to-year variability of the likelihood of E-ring formation is described with PC3 (Fig. 6c). In addition, in Guardamar and Maigmo, PC3 is positively correlated with a possible appearance of RC–LW, while such a relationship is negative in Daroca and Slovenia.

Climatic signals in tree rings

Year-to-year variations in PC1 in all four sites (Fig. 7) are mainly related to the variations of climatic conditions in winter and spring. Thus, high precipitation in winter and spring in Daroca, Guardamar and Maigmo, and high precipitation in June in Slovenia correspond to higher values of PC1. Similarly, high temperatures in winter, but low temperatures in June and July in Daroca and Slovenia correspond to high values of PC1, whereas in Maigmo and Guardamar, PC1 values are higher when the temperatures from April to July are lower.

Year-to-year variations in PC2 are mainly related to year-to-year variations of climatic conditions in summer and autumn (Fig. 7). Precipitation in August and September in Daroca, September in Guardamar, from July to September in Maigmo, and in July and August in Slovenia promote high values of PC2 and are the main climatic factors promoting formation of LW and its density fluctuation.

Finally, in all four sites, PC3 (Fig. 7) is related to contrasting conditions during the transition from humid to dry periods. Thus, PC3 is higher in Daroca if May is dry but July is wet; in Guardamar if March is dry and May is wet; in Maigmo if winter is dry, April is hot, and May is wet; in Slovenia if June is dry and September is wet.

Discussion

Our study in *P. halepensis* demonstrates that the information from tree-ring measurements and those contained in wood anatomical characteristics are highly sensitive to the year-to-year variation in climatic conditions. The highest values of mean sensitivity (MS) of most variables were found for *P. halepensis* in the sites in Spain, while in Slovenia the MS values were considerably lower. This is in agreement with previous studies showing that radial growth of trees in the Mediterranean is highly dependent on climatic conditions during the growing season (Cherubini et al. 2003), while in other more continental, Atlantic or Alpine environments, significant delays are observed

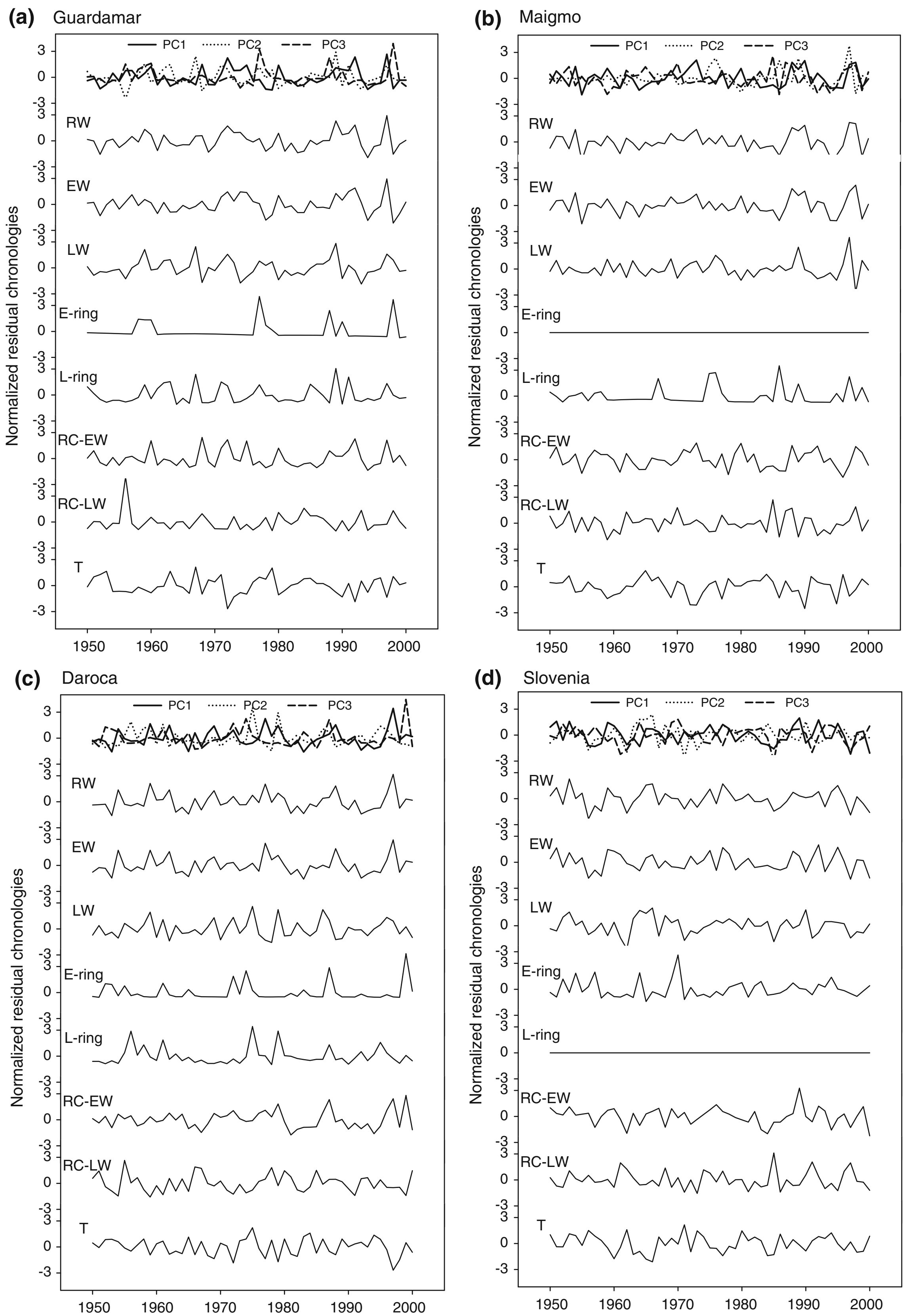

Fig. 5 a–d Significant PCA eigenvectors, normalized residual chronologies of tree-ring measured elements (RW, EW, LW) and normalized residual frequencies of the analyzed wood anatomical features. (E-ring, L-ring, RC–EW, RC–LW, transition) at the four sites studied

Table 3 Total explained variance (%) of principal component factors PC1, PC2 and PC3 derived from RW, EW, LW, E-ring, L-ring, RC–EW, RC–LW and *T* at four sites

	PC1 (%)	PC2 (%)	PC3 (%)
Guardamar	38.3	25.6	13.5
Maigmo	37.6	25.8	12.1
Daroca	36.8	22.8	13.2
Slovenia	34.9	21.0	15.5

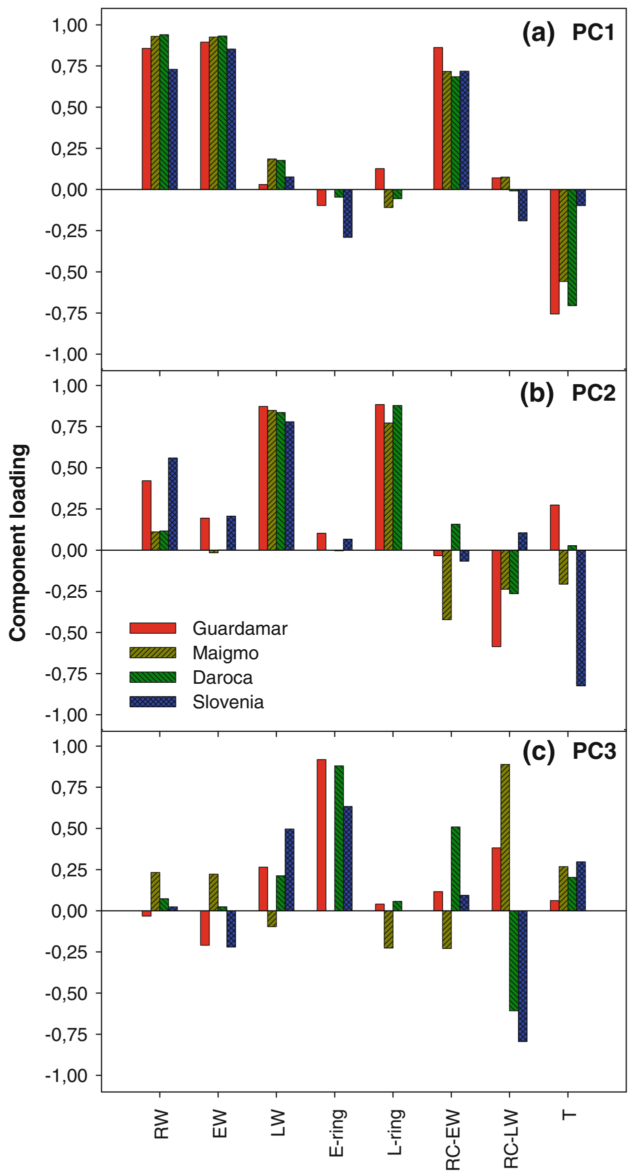

Fig. 6 a–c Loading of principal component factors (PC1, PC2, PC3) at the four sites studied for: tree ring (RW), earlywood (EW) and latewood (LW) widths, E-ring (latewood-like cells in earlywood), L-ring (earlywood-like cells in latewood), RC–EW (resin canals in earlywood), RC–LW (resin canals in latewood), *T* (transition between earlywood and latewood)

(Camarero et al. 1998), and radial growth is more dependent from canopy position (Copenheaver et al. 2006; Hoffer and Tardif 2009; Rozas et al. 2011). Our results show a high sensitivity of trees in a typical Mediterranean climate, which may provide invaluable climatic information.

Despite the high sensitivity we observed, our study indicates that information from various parameters is partially redundant. In all four sites analyzed, the data contained in eight different tree-ring variables can be summarized in just three independent components. For instance, if earlywood is wide, it is more likely that the resin canals will occur in earlywood and that the transition from earlywood to latewood will be gradual. We found that earlywood widths and resin canals of earlywood are correlated in *P. halepensis*. Similarly, if latewood is wider, there is a higher likelihood of L-ring formation. L-ring formation is related to the summer stop and later restart with another growing cycle in autumn, if the conditions are favorable (de Luis et al. 2011a). Such favorable conditions allow larger growing season and, as a consequence, the quantity of latewood increases. Because of this, LW and L-ring are positively correlated, and depend on the same climatic parameters.

Different studies also suggest that the frequency of IADFs is higher in younger/smaller trees, and in trees with higher growth rates than in older/bigger ones (Vieira et al. 2009; Olivar et al. 2012). Our results comparing the IADF frequency observed in different sites do not seem to be in agreement with this hypothesis. The frequency of IADFs was not lower in the study site where the tree rings were narrower (Guardamar), although wider tree rings were observed in the Slovenian site, no IADFs (L-rings) were found in latewood. This contradiction can probably be related to the differences in the seasonal growth pattern of *P. halepensis* in the sites in Slovenia and Spain. Different studies reveal that, under xeric conditions (as observed in our study sites in Spain), the dynamics of cambial activity in *P. halepensis* is characterized by two major growth phases, one in spring and another in autumn (de Luis et al. 2007, 2011a; Camarero et al. 2010). Under these conditions, IADFs (L-ring) were formed as a result of cambial reactivation in autumn triggered by favorable wet conditions (de Luis et al. 2007, 2011a, b). However, under mesic conditions (such as on the Slovenian site), the cambium probably remains active during the summer and the growing season ends in late summer or early autumn due to low temperatures (de Luis et al. 2011a, Camarero et al. 2010) and as a consequence, L-ring are unlikely to be formed.

As demonstrated by Battipaglia et al. (2010) in *Arbutus unedo*, the frequency and the triggering climatic factors promoting different anatomical characteristics may vary

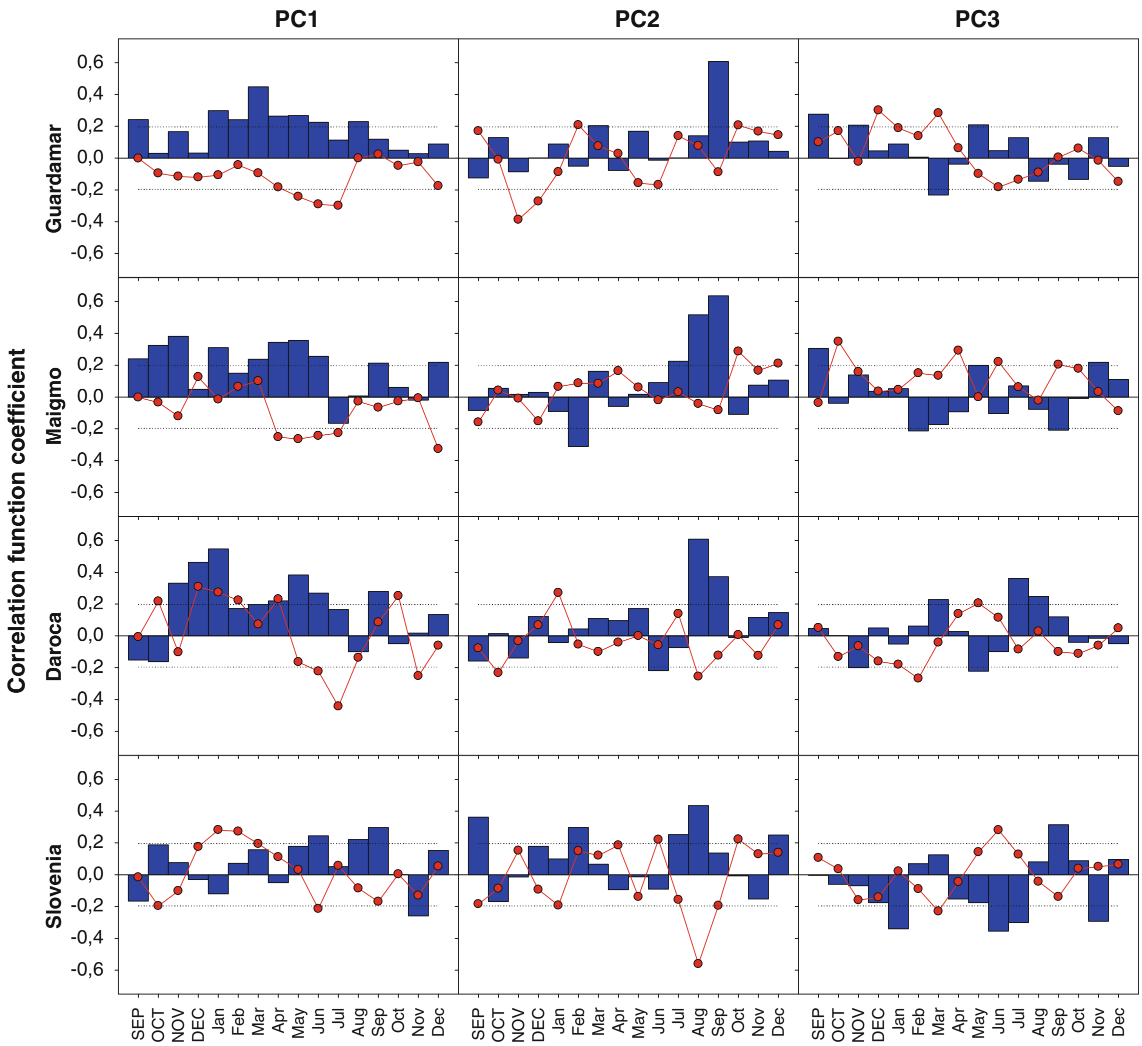

Fig. 7 Climatic interpretation of principal component factors (PC1, PC2, PC3) at the four sites studied. The horizontal axis shows the months from September of the previous year to December of the current year. The *vertical axis* shows the correlation function coefficients, and significant correlation values are marked by *two horizontal lines* on either side of $y = 0$. *Blue bars* are correlations with total monthly precipitations (in mm) and the *red line* represents correlations with the average annual temperature (in °C)

among populations, depending on different environmental conditions. In this respect, our study shows that the occurrence of three independent groups of characteristics described by three principal components is modulated by different climatic elements at each of the sites studied. However, in all four sites, each group of tree-ring characteristics mainly reflects the influence of climatic conditions occurring during the same growing phases (PC1 is mainly related to climatic conditions in winter and spring and to earlywood characteristics; PC2 mainly depends on climatic conditions during summer and autumn and is related to latewood characteristics; PC3 is mainly related to climatic conditions during the transition from the wet to dry periods during the growing season). Furthermore, for PC1, there is a kind of gradual transition among the sites. PC1 is strongly correlated with January to March precipitation in Guardamar, whereas it is correlated with precipitation from the previous autumn and April to June of current year in Maigmo. In Daroca, PC1 is quite similar to Maigmo, whereas in Slovenia, the main limiting factor is January–February temperature. Thus, the winter and spring climatic conditions are important for earlywood growth. The present study also reveals that the anatomy of earlywood and latewood is mainly determined by the prevalent climatic conditions during their formation. Significant delays between the triggering factors and the formation of anatomical features, as described in conifers growing at higher elevations, seem to be less clear under Mediterranean conditions (Camarero et al. 1998).

The influence of different seasonal climate elements is integrated into tree-ring width, but since such seasonal climatic elements are correlated among themselves, the isolation of the individual climate relationships is difficult to determine. We found that EW and LW measurements and also the frequency of intra-annual anatomical characteristics vary in relation to the particular seasonal climate conditions. Our study reveals that the combined information of tree-ring widths and anatomical characteristics can help us better to interpret and identify the influences of seasonal climate on the development of *P. halepensis* tree-rings. Since the results can be generalized across a wide range of environmental conditions, the information contained in tree-ring structure may be a valuable proxy for studies on a regional scale.

According to our results, global warming or any other modification in seasonal climatic regimes, apart from modifying the growth rates, may also induce changes in wood structure. The changes in the earlywood and/or latewood widths, for example, may result in modifications of the hydraulic and mechanical properties of wood that may affect water transport and plant survival (Froux et al. 2002; De Micco et al. 2008; Martinez-Meier et al. 2008). The ability of species to produce different types and forms of cells in different periods may also be interpreted as an important adaptation of trees for maintaining the balance among the capacity to conduct water, resistance to cavitation and mechanical stability. All this could play an important role in acclimatization or/and adaptation to new, changed climatic conditions.

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