

Environmental control of vessel traits in *Quercus ilex* under Mediterranean climate: relating xylem anatomy to function

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Abstract Time series of tree-ring anatomical features are important to understand the functional role of xylem plasticity over the life span of trees, and thus to reconstruct past ecological and climatic conditions. Holm oak (*Quercus ilex* L.) is a drought-tolerant tree widely distributed in the Mediterranean Basin. Chronologies of tree-ring width (TRW), vessel lumen area [maximum (MAX) and mean (MVA)] and vessel density (VD) were developed for the period 1942–2001. Each ring was divided into three sections to compare the intra-annual variation of vessel features with the climate conditions during the growing season. The common variability of tree-growth and vessel features was analyzed using a principal component analysis (PCA). Vessel lumen area (MAX and MVA) and TRW loaded positively on the first axis (PC1), whereas VD from the first and second part of the ring (VD1 and VD2) loaded negatively, suggesting that these variables share a common variance. On the other hand, VD in the last third of the ring (VD3) loaded positively on second axis (PC2). PC1 showed a strong positive correlation with precipitation during the hydrological year (prior October–September) and a negative correlation with temperature in spring (April–May), while PC2 showed a negative correlation with precipitation in June. Our results showed that TRW and vessel lumen area were mainly dependent on moisture

conditions along the growing season, while vessel density probably plays an important role in the balance between hydraulic conductivity and safety to embolism to better adjust the hydraulic system to water availability.

Keywords Holm oak · Mediterranean climate · Ecological wood anatomy · Vessel lumen area · Vessel density

Introduction

Tree-ring width (TRW) is traditionally used as the main feature to describe radial growth and have already proven to be a good proxy of past climate conditions (Fritts 2001). Since the early 1980s, other wood anatomical features with a higher temporal resolution, such as vessel (or tracheid) lumen area and vessel density, have also been used as climatic proxies (Schume et al. 2004; Tardif and Conciatori 2006; Kames et al. 2011). The increasing number of dendrochronological studies using cell features is partly explained by the development of less time-consuming wood surface preparation techniques and semi-automated image programs, and also because cell parameters may improve climate reconstructions from tree-ring width (Fonti and García-González 2008; Fonti et al. 2010; Campelo et al. 2010).

Among the studies that have used cell features as environmental proxies, there are methodological differences when studying softwood and hardwoods. The so-called tracheidogram method has been used to identify growth conditions in softwood species on the basis of the diameter and wall thickness of tracheids. In hardwoods, the study of different sections within annual rings was used to study the influence of environmental conditions on vessel

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lumen area throughout the growing season (Sass and Eckstein 1995). Later, the concept of tracheidograms was applied to analyze vessels in hardwoods, designated by tracheogram method, which relate vessel features to climate (Schume et al. 2004; Grabner 2005). The tracheograms were successfully used to relate the intra-annual variation of vessel lumen area with climate or hydrological conditions during the growing season (Grabner 2005).

Time series of wood cell parameters and its relation with climatic conditions can also deepen the knowledge on the functional role of xylem anatomy. The pattern of vessel distribution is characteristic of the species and thus genetically determined (Mather et al. 1993; Fisher et al. 2007; Coccozza et al. 2011). However, the environmental conditions also have a strong influence on the build-up of the tree ring, the reason why cell features also record climatic conditions along the growing season. Abundant water supply promotes the formation of large vessels directly, by a high turgor pressure and a rapid vessel expansion (Tyree and Sperry 1989; Sass and Eckstein 1995), and indirectly, by lowering the auxin concentration and thus slowing differentiation and allowing more vessel expansion (Kozłowski and Pallardy 1997; Aloni 2001). Vessel lumen area strongly affects the capacity of xylem to conduct water (Zimmermann 1983). Thus, the wide vessels produced in the beginning of the growing season are more efficient in water transport, when moisture conditions are appropriate. In addition, there is a clear trade-off between conduit diameter and the susceptibility to cavitation, with larger vessels more vulnerable to cavitation (Sperry et al. 2006). Although this relationship is clear in freezing-induced cavitation, it is ambiguous in drought-induced cavitation (Hacke and Sperry 2001). It seems that drought-induced cavitation depends more on pit membrane pore diameter, which seems partially uncoupled from conduit diameter (Tyree and Sperry 1989; Hacke and Sperry 2001).

According to the Hagen-Poiseuille law the hydraulic efficiency of a vessel increases proportionally to the 4th power of its radius, thus a small decrease in the mean vessel diameter causes a considerable decrease in hydraulic efficiency (Zimmermann 1983). One way to compensate this reduction in hydraulic efficiency is to increase the vessel density (Schume et al. 2004) and the variation in the ratio of MVA/VD is a strong driver of sapwood-specific hydraulic conductivity (Zanne et al. 2010). Nonetheless, the number of vessels in a given transverse area should have a relatively small effect on sapwood conductance (Preston et al. 2006). Although closely spaced vessels (high density) may enhance conductivity when water is available, it can also increase the spread of embolism when cavitation occurs (Carlquist and Hoekman 1985; Hacke and Sperry 2001). Very small vessels together with low vessel density appeared to be associated with resistance to xylem

cavitation under tension, while larger and denser vessels were generally found among drought-deciduous species (Preston et al. 2006).

Contrary to the clear environmental signal found in the lumen area of vessels, reports in the literature give contradictory results concerning vessel density. According to Sass and Eckstein (1995), the density of vessels in the diffuse porous beech tree (*Fagus sylvatica* L.) “is nearly constant throughout the tree ring, leading to the assumption that vessel density does not provide much information on external influences”. *Quercus suber* L., a semi-ring porous species growing under Mediterranean climate, also showed a vessel density along the growth ring nearly constant (6 vessels/mm²) (Leal et al. 2011). Conversely, Schume et al. (2004) found that vessel density in hybrid poplars was more sensitive to hydrological alterations than vessel lumen area. Additionally, Corcuera et al. (2004) observed a positive correlation between vessel density in branches of *Quercus ilex* L. and precipitation in January and April, but no ecophysiological interpretation was given.

Quercus ilex (holm oak), a semi-ring to diffuse porous tree (Schweingruber 1990; Campelo et al. 2010), is a long-lived (Panaiotis et al. 1997; Patón et al. 2009) and drought-tolerant species (Terradas and Savé 1992; Montserrat-Martí et al. 2009) widely distributed in the Mediterranean Basin, being the dominant evergreen oak in the western part (Barbero et al. 1992; Terradas 1999). Wood anatomical features of *Q. ilex* showed variations in response to extreme droughts (Corcuera et al. 2004) and water availability along a rainfall gradient in North-East Spain (Villar-Salvador et al. 1997), suggesting that water use of this species is partly regulated by xylem anatomical adjustments. Although *Q. ilex* and *Q. suber* often coexist in Portugal, *Q. ilex* mainly occurs in the drier (inland) area, where soils are shallower and summer aridity is the main limiting factor, whereas *Q. suber* dominates in the coastal areas (wetter). In inland areas, trees could show a “quiescent” phase during the hot and dry summer (Gutiérrez et al. 2011) and cambial activity could resume when water deficits are alleviated by autumn rains, with the formation of false rings (Campelo et al. 2007).

In this study, we consider the variation of TRW and vessel traits [maximum vessel area (MAX), mean vessel area (MVA) and vessel density (VD)] and its correlation with climatic conditions, in a 60-year chronology of *Q. ilex*. Each ring was divided into three sections to better compare the intra-annual variation of vessel features with the climate conditions during the growing season. We hypothesize that the climatic information of the vessel lumen area is similar to the TRW and controlled by water availability during the growing season. We also hypothesize that vessel density is more sensitive to climatic conditions in the middle of the growing season, when the

decrease in vessel lumen area and the associated reduction in hydraulic efficiency can be compensated by an increase in vessel density.

Materials and methods

Study area and climate

The study area was located in the Alqueva region, near the Guadiana river (southeast Portugal; 38°36'N, 7°15'W, 140 m a.s.l.). Before the construction of the Alqueva dam, which created the largest artificial lake in Europe, this area was characterized by a human managed forest of holm oak, named 'Montado'. All the vegetation was cut down before the Alqueva reservoir started to fill in 2002.

The climate is Mediterranean, with a mean annual temperature of 16.1 °C and a total annual precipitation of 601 mm (average data from the three nearest meteorological stations: Amareleja 38°12'N, 7°12'W, 192 m a.s.l.; Elvas 38°54'N, 7°12'W, 208 m a.s.l.; and Évora 38°30'N, 7°48'W, 308 m a.s.l.). Rainfall mainly occurs from October to April, with a dry period in summer.

Wood preparation and vessel measurements

In a previous work (Campelo et al. 2009), 30 cm above-ground cross sections of 20 trees, cut down before the filling of the Alqueva dam, were used to study the climatic signal of the TRW. In the present study, we have selected 11 out of these 20 trees, excluding trees with less than 60 years or with many tyloses, and analyzed one cross-section per tree.

Tree rings were visually crossdated; TRW was measured and the visual crossdating was statistically confirmed using the program COFECHA (Holmes 1983). The samples were prepared for vessel measurements according to Sass and Eckstein (1994). First, wood dust and tyloses were removed from vessel lumen with a high-pressure water blast. Afterwards, vessels were filled with white chalk to increase the contrast between vessel lumen and the ground tissue. Images of the cross-section surface were captured on a radial path from the bark to the pith using a digital camera (Nikon DMX 1200F) attached to a stereomicroscope. The tangential width of these sections was larger than 7 mm.

ImageJ software was used to analyze the digital images (<http://rsbweb.nih.gov/ij/>). Tree-ring limits were identified by the differences in vessel lumen area and by the marginal parenchyma bands (Campelo et al. 2007). These limits and wood rays were used to establish, respectively, tangential and radial boundaries of sections analyzed for vessel

measurements. For each tree ring, vessel lumen areas were measured. Size (1,500–80,000 μm^2) and shape (objects with a width/length ratio equal or lower than 0.60 were excluded) filters were defined to remove objects that were not vessels. Misrecognized vessels were manually corrected. Such corrections consisted of adding non-recognized vessels, deleting misrecognized vessels, splitting clustered vessels and correcting misrecognized vessel contours. After all manual corrections and before the measurement of the lumen area, vessel outlines were smoothed to an elliptical shape (Fig. 1). To determine the relative radial position of each vessel within the tree ring, the coordinates of its centroid were recorded.

Data analysis

The period for the analysis was 1942–2001 (60 years). To separate vessels formed during different periods, each tree ring was radially divided into three equal parts (Fig. 1).

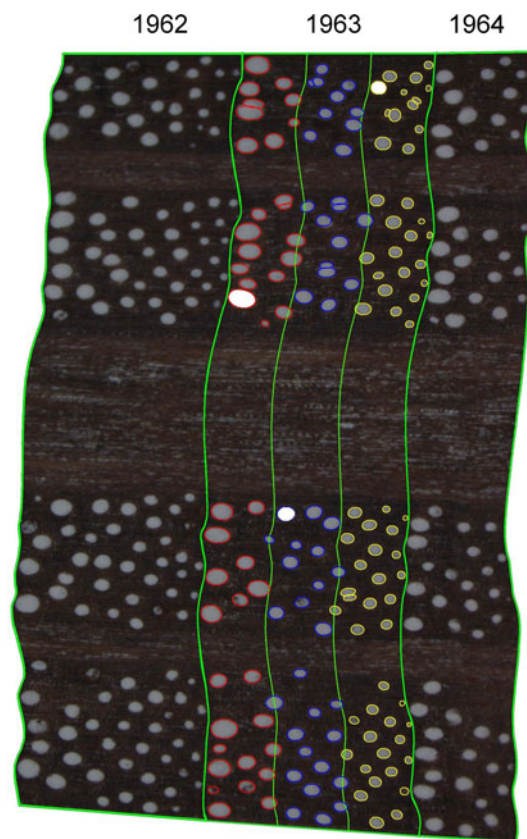


Fig. 1 Example of an image of *Quercus ilex* wood surface used to determine the lumen area of vessels and their position within the ring. Green lines are used to delimit tree rings (1962–1964) and also to radially divide the ring 1963 into three equal parts. Vessels of the first, second and third sections are bounded by red, blue and yellow contours, respectively. The largest vessel of each third is white filled (color figure online)

Maximum vessel lumen area (MAX), mean vessel lumen area (MVA) and vessel density (VD) were determined for each one.

Chronologies of TRW and vessel variables (MAX, MVA and VD) were obtained from individual time series. Non-climatic growth trends, associated with low-frequency variability, were estimated by fitting a cubic smoothing spline with a 50 % frequency cut-off of 32 years, and removed by dividing the original data by the fitted curve (Cook and Peters 1981). The growth indices obtained were averaged to build standard chronologies. The statistical quality of chronologies was evaluated using four parameters commonly applied in dendrochronology: mean correlation between trees (R_{bt}), expressed population signal (EPS), mean sensitivity (MS) and first-order autocorrelation (AR_1) (Wigley et al. 1984; Briffa and Jones 1990; Fritts 2001). The EPS value measures how well a chronology based on a finite number of trees represents the hypothetical population chronology, so that the higher the R_{bt} and the sample size, the higher is the EPS.

Principal components analysis (PCA) was used to describe patterns of co-variation among vessel features (MAX, MVA and VD) and TRW. The significant principal components were selected according to the Kaiser's rule (eigenvalue >1 ; Kaiser 1960). The relation between the significant principal components and monthly meteorological data (temperature and precipitation), from October of the previous year ($t - 1$) to November of the current year (t), was analyzed by Pearson's correlation coefficients. Additionally, the climatic signal was also investigated for the period between October_(t-1) and September_(t) (the hydrological year) and for a 2-month span from April_(t) to May_(t), when *Q. ilex* shows the maximum radial growth (Gutiérrez et al. 2011).

Results

The lumen area of all measured vessels ($n = 54,926$) had a mean value of $10,510 \mu\text{m}^2$ and ranged from $1,291$ to $77,547 \mu\text{m}^2$. Their frequency distribution was skewed to the left, with few large vessels and many small vessels (Fig. 2a). More than half of the vessels (57.5 %) were smaller than $10,000 \mu\text{m}^2$ and only 4.8 % showed a lumen area larger than $25,000 \mu\text{m}^2$. Although small vessels occurred throughout the whole ring, large vessels were more frequent at the beginning and vessel lumen area decreased gradually across the ring (Figs. 1, 2b).

The variables MAX, MVA and VD (considering the whole ring) were strongly correlated ($r \geq 0.82$; $p < 0.001$) with MAX1, MVA1 and VD1, respectively. For this reason, MAX, MVA and VD for the entire ring were not considered for further analyses.

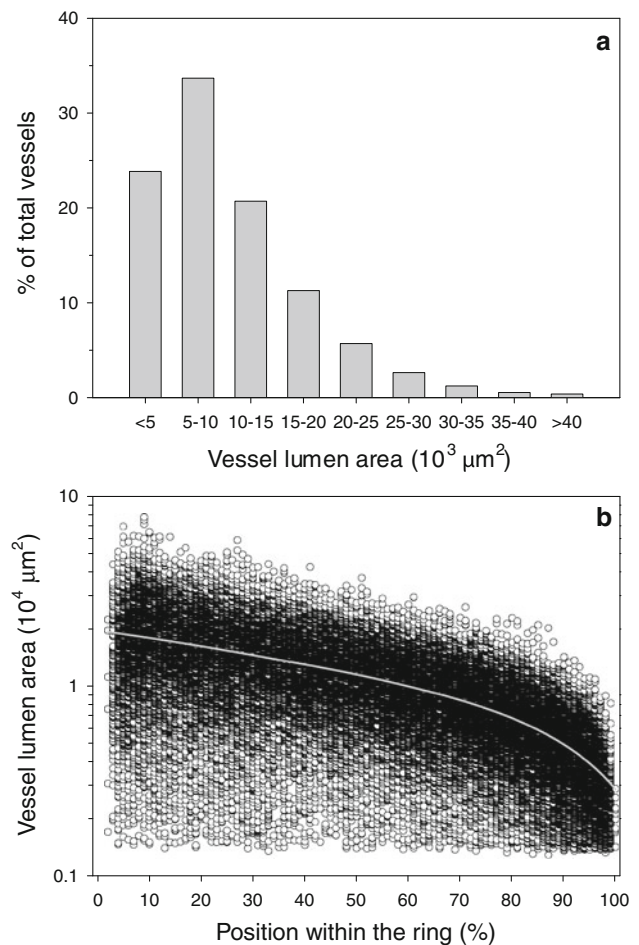


Fig. 2 a Frequency distribution of vessel lumen area classes of *Quercus ilex*. b Distribution of all measured vessel lumen areas across the ring; the gray line represents the smoothing curve with a span width of 0.70

In the detrended series, where only high-frequency variation was retained, the growth index of TRW showed a higher year-to-year variation compared to the growth indices of vessel variables (Fig. 3). A high common signal was found for TRW, while all vessel variables yielded EPS values lower than the critical value of 0.85 proposed by Wigley et al. (1984) (Table 1). The values of EPS for vessel lumen area variables (MAX and MVA) were higher than those of VD. The TRW had a higher year-to-year variation (higher MS values) than vessel variables. All variables were not significantly affected by previous growth (very low AR_1 values).

The first two axes of the PCA explained 68 and 12 % of the variation in the ten included variables, respectively (Fig. 4). Vessel lumen area variables (MAX and MVA) loaded strongly on the first axis, along with negative loadings of vessel density (VD1 and VD2). Vessel density of the last portion of the ring (VD3) loaded strongly on the second axis (Fig. 4). The vectors for MAX2, MVA2 and VD2 were nearly orthogonal to the VD3 vector.

Fig. 3 Raw and standardized chronologies of tree-ring width (TRW), and of maximum vessel area (MAX), mean vessel area (MVA) and vessel density (VD) of each third of the ring (1, 2 and 3), for the period 1942–2001

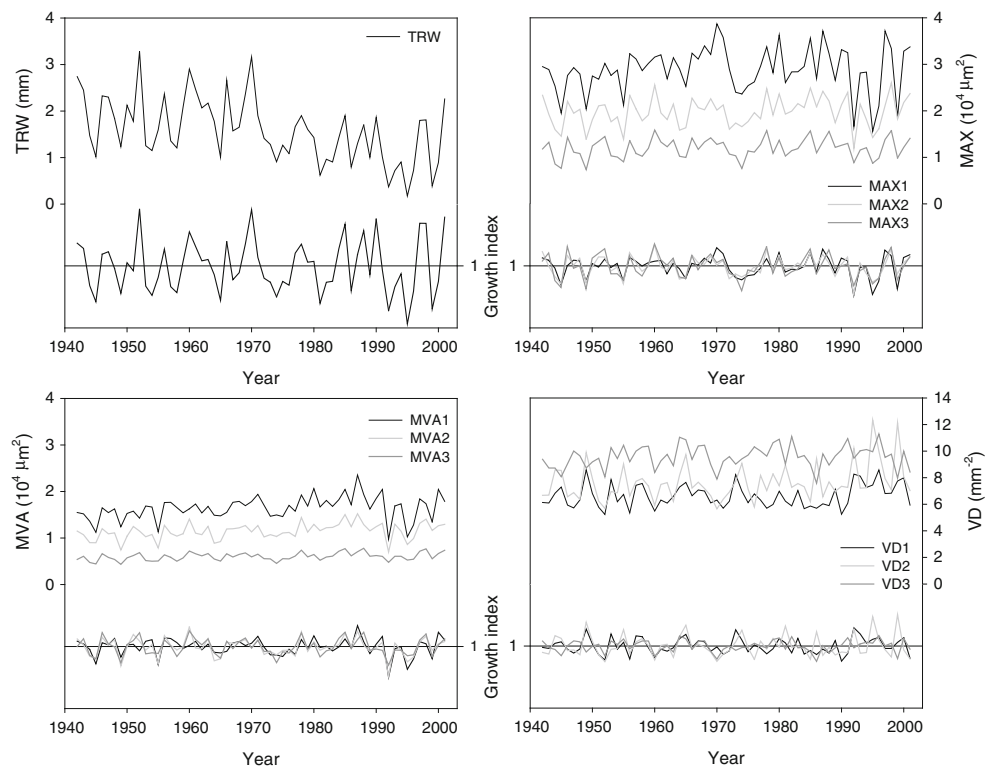


Table 1 Correlation between trees (R_{bt}), expressed population signal (EPS), mean sensitivity (MS) and first-order autocorrelation (AR_1) for tree-ring width (TRW), and maximum vessel area (MAX), mean vessel area (MVA) and vessel density (VD) of each third of the ring (1, 2 and 3), for the interval 1942–2001

	TRW	MAX			MVA			VD		
		1	2	3	1	2	3	1	2	3
R_{bc}	0.56	0.27	0.26	0.32	0.21	0.32	0.29	0.16	0.20	0.10
EPS	0.93	0.78	0.77	0.82	0.72	0.82	0.80	0.65	0.71	0.53
MS	0.45	0.17	0.18	0.20	0.15	0.15	0.14	0.12	0.18	0.10
AR_1	0.10	0.04	-0.09	0.02	-0.03	-0.07	0.10	0.05	-0.11	-0.02

Regarding the climatic signal of the first two axes of the PCA, PC1 showed significant positive correlations with precipitation in November_(t-1), January_(t), April_(t) and May_(t), with a strong positive correlation with precipitation during the hydrological year (October_(t-1)–September_(t)) and a negative correlation with April_(t)–May_(t) temperatures (Fig. 5). PC2 showed a negative correlation with precipitation in June_(t) (Fig. 5).

Discussion

The goals of this study were to decompose the climatic information present in TRW and vessel features (lumen area and density) in a 60-year old chronology of *Q. ilex*,

and to relate the variability of these anatomical features with climatic conditions and hydraulic traits.

The PCA analysis loaded on the first axis TRW, MAX1-3, MVA1-3, VD1 and VD2 meaning that these variables have similar information. The correlation analysis of the first axis of the PCA with climatic information showed that precipitation in late autumn/winter and spring had a positive effect on TRW and vessel lumen area, with a negative effect on VD1 and VD2. The refill of soil water reserves during winter and high precipitation during the growing season are major determinants for tree growth. This was also observed in previous studies with *Q. ilex* using TRW time series (Zhang and Romane 1991; Nabais et al. 1998–1999; Cherubini et al. 2003; Corcuera et al. 2004; Campelo et al. 2009). It is well known that vessel lumen

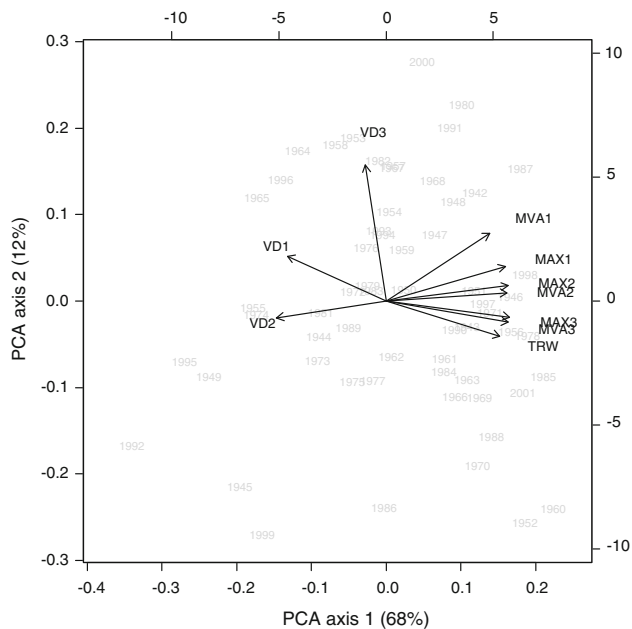


Fig. 4 Position of tree-ring variables (TRW, MAX1-3, MVA1-3 and VD1-3) on the first and second axes of a principal components analysis (PCA). Gray values indicate the loadings of individual years on these axes

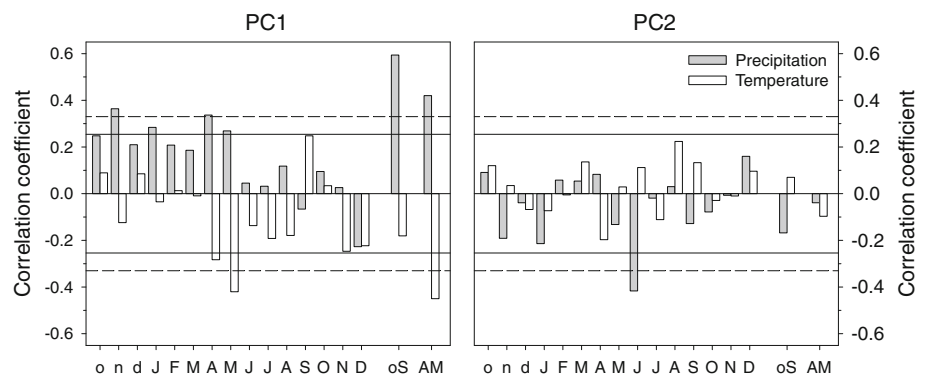
area increases with the availability of water due to a high turgor pressure and rapid cell expansion (Tyree and Sperry 1989). In years with low availability of water during the growing season, smaller vessels are produced, but at a higher density, probably to compensate the loss of hydraulic conductivity (Schume et al. 2004). Thus, the variability of vessel density in the first and second portion of the ring can be used to balance hydraulic conductivity and safety to embolism.

As the season progresses and water availability decreases, the lumen area of vessels tends to decrease, being the vessel lumen area in the last part of the ring strongly determined by the hydrological year. In fact, the strong correlation between TRW, MAX3 and MVA3 indicates a lag effect of early climatic conditions on the vessel lumen area in the last part of the ring. Thus, at the beginning of

the growing season, environmental conditions, such as moisture supply, do not limit growth as much as towards the end of the season (Sass and Eckstein 1995).

The only variable that strongly loaded on the second axis of the PCA was VD3, with a negative correlation with June precipitation. This climatic signal of VD3 was not found in the other variables, although it is puzzling to explain its ecophysiological meaning. Under Mediterranean climate, June is the beginning of the dry season, usually associated with a ‘quiescent’ metabolic phase in *Q. ilex* (Cherubini et al. 2003; Gutiérrez et al. 2011). Thus, whenever June precipitation is higher, vessel density in the last portion of the ring is lower. Theoretically, fewer wider vessels are more efficient in water conductivity than more, narrower ones (Zanne et al. 2010). However, VD3 showed no significant correlation with MAX3 and MVA3, and the recognized negative relationship between vessel lumen area and number (Tyree and Zimmermann 2002; Sperry et al. 2008) was not directly verified in the last portion of the ring. It seems that the variability of VD3 is not ‘used’ to regulate hydraulic efficiency, as hypothesized for VD1 and VD2. We hypothesize that in *Q. ilex* the vessel density in the last portion of the ring is related with the more or less available space outside the vessels with tissues for water storage (Zanne et al. 2010). Probably, the formation of more storage tissues has a trade-off, since it is less expensive to produce vessels, and this is apparently regulated by June precipitation. The possibility to increase stem water reserves before the dry period can buffer leaf water potentials against water shortage, allowing gas exchange and carbon gain to be maintained for more prolonged periods (Stratton et al. 2000; Scholz et al. 2007). This can be especially important to evergreen species, such as *Q. ilex*. The high drought tolerance of the xylem, associated with evergreenness, increases the capacity for rapid utilization of autumn rains for more carbon gain, without waiting for the production of new leaves (Ackerly 2004). In fact, vessel lumen area (MAX and MVA) showed an almost significant correlation with the temperature in September, probably related with the second growth peak of *Q. ilex*.

Fig. 5 Pearson correlation coefficients performed between the two principal components (PC1 and PC2) and monthly data from prior October to current December. Lowercase prior year months; capitals: current year months; oS hydrological year (prior October to current September); AM April–May



In conclusion, the variables TRW, MAX and MVA showed common climatic information, with a positive correlation with autumn/winter and spring precipitation, while VD3 showed a strong negative correlation with precipitation in early summer. It is important to note that, from the ten variables used, VD2 and VD3, which are nearly orthogonal, integrate the main climatic signals present in tree rings of *Q. ilex* from our study area. Vessel density can be important to balance hydraulic conductivity and safety to embolism, especially in the second part of the ring, when mean vessel area starts to decrease. In the last part of the ring, vessel density is probably important to increase, or decrease, the tissues used for water storage. The extensive distribution of *Q. ilex* across the Mediterranean Basin makes this species unique to explore the link between climate variability, xylem anatomy and hydraulics, to further understand xylem plasticity in trees (Fonti and Jansen 2012).

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