Xylem hydraulic adjustment and growth response of *Quercus canariensis* Willd. to climatic variability

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Global change challenges forest adaptability at the distributional limit of species. We studied ring-porous *Quercus canariensis* Willd. xylem traits to analyze how they adjust to spatio-temporal variability in climate. Trees were sampled along altitudinal transects, and annual time series of radial growth (ring width (RW)) and several earlywood vessel (EV) traits were built to analyze their relationships with climate. The trees responded to increasing water constraints with decreasing altitude and changes in climate in the short term but the analyses showed that xylem did not acclimate in response to long-term temperature increase during the past 30 years. The plants’ adjustment to climate variability was expressed in a different but complementary manner by the different xylem traits. At low elevations, trees exhibited higher correlations with water stress indices and trees acclimated to more xeric conditions at low elevations by reducing radial growth and hydraulic diameter ($D_H$) but increasing the density of vessels (DV). Average potential conductivity ($K_H$) was similar for trees at different altitudes. However, inter-tree differences in xylem traits were higher than those between altitudes, suggesting a strong influence of individual genetic features or micro-site conditions. Trees exhibited higher RW those years with larger $D_H$ and particularly the linear density of vessels (DVl), but partly, climatic signals expressed in RW differed from those in EVs. Trees produced larger $D_H$ after cold winters and wet years. Ring width responded positively to wet and cool weather in fall and spring, whereas the response to climate of DV and $K_H$ was generally opposite to that of RW. These relationships likely expressed the negative impact of high respiration rates in winter on the carbon pools used to produce the EVs in the next spring and the overall positive influence of water availability for trees. Our results showed that trees at different sites were able to adjust their hydraulic architecture to climatic variability and temperature increase during recent decades coordinating several complementary traits. Nonetheless, it should be monitored whether they will succeed to acclimate to future climatic scenarios of increasing water stress.

**Keywords:** conductivity, dendroecology, global warming, Mediterranean, tree-rings, vessels.

Introduction

Climate warming is likely to be fatal for some plant species at xeric locations in drought-stressed ecosystems. Most climate predictions indicate increasing water stress in many regions (IPCC 2007). Thus, understanding the susceptibility of tree populations to drought is crucial to ensure the best forest management to foster their preservation, particularly at species’ lower altitudinal and latitudinal distribution limits (McDowell et al. 2008, Allen et al. 2010). Species have different physiological and xylem adaptive strategies, which in part determine their ecological niche (Brodribb and Hill 1999). Plants with contrasting xylem attributes may, however, coexist within communities subject to similar water stress (Martínez-Vilalta et al. 2002). For this reason, it is important to investigate the variability of functional characteristics and vulnerability to water stress of different xylem types.

According to optimal carbon allocation models, plants produce stems that maximize conductivity and minimize wood
density, while ensuring appropriate mechanical stability (Hacke and Sperry 2001, Preston et al. 2006, Zanne et al. 2010). In principle, under dry conditions, i.e., higher cavitation risk, trees tend to form smaller conduits and have greater wood density (Hacke and Sperry 2001, Preston et al. 2006, Poorter et al. 2010, Zanne et al. 2010). In angiosperms the water pressure necessary to cause cavitation is inversely related to the total area of pits in the conduit, which increases with vessel width (Hacke and Sperry 2001, Tyree and Zimmermann 2002, Cai and Tyree 2010). Trees reduce risks from negative water potentials and xylem cavitation through stomata regulation, which limits carbon assimilation and hydraulic conductivity (Hubbard et al. 2001, Mencuccini 2003). Therefore, a trade-off exists between hydraulic efficiency and resistance to dry conditions (Fichot et al. 2011). Tree traits are plastic, yet the xylem can adjust to external forcing within certain limits and vulnerability to drought increase is species specific (Martinez-Vilalta et al. 2009, Brodribb et al. 2010). Trees modify their xylem hydraulic architecture as a response to climate in the short and the long term, and annually resolved dendrochronological time series of wood traits can be used to study the spatio-temporal adjustment of trees to external forcing factors such as climate (see Fonti et al. 2010 for a review). This adds the temporal scale to studies of xylem functional traits, which often lack analyses of interannual variability (e.g., Preston et al. 2006, Martinez-Vilalta et al. 2009, Fichot et al. 2009, Umebayashi et al. 2010, Zanne et al. 2010).

In ring-porous angiosperms large earlywood vessels (EVs) play a major role in water transport (Granier et al. 1994, Tyree and Zimmermann 2002, Taneda and Sperry 2008). Ring porosity is an adaptation that allows high conductance during warm, humid springs while tolerating annual cavitation caused by freeze–thaw events (Sperry et al. 1994, Cavender-Bares and Holbrook 2001). Large vessels allow very efficient water transport, but their size also increases their susceptibility to embolism (Cochard and Tyree 1990, Hacke and Sperry 2001). Large EVs are produced every year to restore hydraulic conductance because they irreversibly cavitate within the year after formation (Cochard and Tyree 1990, Sperry et al. 1994). Thereafter, sap is assumed to be conducted by much smaller, yet more abundant, latewood vessels, which can be functional in several older rings to maintain xylem hydraulic efficiency (Granier et al. 1994, Umebayashi et al. 2010). Production of earlywood largely occurs before leaf-out with carbon stored during the previous growing season (Barbaroux et al. 2003, Hoch et al. 2003), whereas radial growth often shows a response to longer periods of climate (e.g., Cook and Kairiukstis 1990).

Plant growth in Mediterranean environments is challenged by irregularly distributed precipitation and reduced water availability in summer, but also locally by low temperatures in winter (‘double-stress’. Mitrakos 1980, Cherubini et al. 2003). The hydraulic architecture of plants growing in such harsh environments should maximize water transport to sustain photosynthesis during favorable conditions, i.e., mild and humid early spring and fall, while reducing the risk of vessel failure when conditions are unfavorable, i.e., during cold winters and dry summers (Villar-Salvador et al. 1997, Baldocchi et al. 2010, Vaz et al. 2010). Quercus canariensis Willd. is a ring-porous and facultative winter-deciduous oak species, which only occupies sites characterized by the most humid and warm variants of the Mediterranean climate in Iberia and Northern Africa (Costa et al. 2005). Thus, we expect the species to be particularly sensitive to increases in aridity such as those predicted for the area in the near future (IPCC 2007). Despite its high ecological importance this species has been seldom utilized in dendroecological studies, which only include African populations (e.g., Aloui and Serre-Bachet 1987, Messaoudene and Tessier 1991, Tessier et al. 1994). Several authors report a negative impact of the overall increase in water stress suffered in recent decades in the Mediterranean on the performance of some species at the limit of their distribution (e.g., Peñuelas and Boada 2003, Piovesan et al. 2008, Sarris et al. 2011). Here we study how different xylem traits of Q. canariensis, such as ring width (RW) and anatomical vessel features (EVs), adjust in space along altitudinal gradients including the local low elevation limits for the species distribution, and, in time, with increasing temperature. Chronologies of RW and hydraulically relevant EV traits were produced for different sites to analyze how trees modify their xylem traits in the short and long term as a response to climate variability at sites with different climates.

Material and methods

Site and tree characteristics

A total of 98 dominant Quercus canariensis Willd. trees from either monospecific or mixed stands with Quercus suber L. were sampled at different elevations in Southern Spain and Northern Tunisia. In Southern Spain, samples were collected from three plots (ALClow, ALCmid, ALChigh), located along an altitudinal transect from 330 to 930 m a.s.l. on a slope in Los Alcornocales Natural Park. In Tunisia, trees were sampled at two sites with elevations ranging from 640 to 940 m a.s.l. (TUNlow, TUNhigh, Figure 1, Table 1) on a slope in Al-Feidja National Park. These two altitudinal transects covered the whole local distributional range for the species including the local minimum and maximum altitude where the species is dominant. Higher temperatures and lower precipitations at lower altitudes lead to increased water stress conditions, forcing the local lower altitudinal distribution limit for the species (i.e., where we established the low elevation plots). Below these lower elevations there are just evergreen-dominated
woodlands or semiarid shrubland communities. Therefore, the sampled altitudinal gradients coincide with climatic gradients of decreasing overall water stress conditions with increasing altitude. Considering a mean lapse rate of 0.6 °C for every 100 m in elevation (Nobel 2009), mean temperature difference between ALClow and ALChigh would be 3.6 °C, and 1.2 °C between TUNlow and TUNhigh.

Measurement of RW and EV traits

Two cores were taken at 1.3 m from each selected tree, and the stem diameter and tree height were measured. Cores were air dried, fixed on wooden mounts, sanded and RW measured. Ring-width series were visually cross-dated and the dating was checked using COFECHA (Holmes 1983). Ring-width indices were obtained by removing the age trend using 30-year individual splines and autocorrelation before computing the final indices using the ratio between the observed and expected annual mean growth (Table 2, Cook and Kairiukstis 1990). We used individual detrending with a flexible spline to remove the non-climatic low-frequency noise derived from management in the sampled stands, although this will also remove the low-frequency climatic signal (Fritts 1976). To compare the quality of the chronologies, we calculated regularly used statistics such as the mean sensitivity (MS) to reflect the high-frequency variance; the mean expressed population signal (EPS), which is the chronology signal expressed as a fraction of the total chronology variance; the mean first-order autocorrelation on the growth series (AR(1)); and the mean correlation between all individual series (Rbt) (Fritts 1976, Cook and Kairiukstis 1990). When cores did not reach the pith, ages were corrected proportionally to the growth of the youngest 20 annual rings measured (Rozas 2003).

Vessel measurements were then performed over the period 1975–2008 on a subsample of at least 11 cross-dated cores (Table 3) from each of the five sites. Only trees older than 75 years were selected to avoid the effect of juvenile wood, i.e., smaller vessels as a consequence of reduced tree height (Tardif and Conciatori 2006, Fonti et al. 2010). To measure the vessel anatomical traits, subsamples of the same cores mounted on wooden devices and sanded for RW measurements were cleaned with an air–water blast and stained with black ink. The vessels were filled with white chalk (Figure 2) and the cores were scanned with 2400 dpi resolution for
Table 2. Characteristics of the mean tree ring chronologies. Ring width (mm, RW), standard deviation (Std), mean sensitivity (MS) and AR(1) are the series averages. EPS (expressed population signal) and Rbt (correlation between trees) were calculated for the mean chronology and indices. Length is the period with five or more series, and those years were included in the final chronologies (see Supplement S2 available as Supplementary Data at Tree Physiology Online).

<table>
<thead>
<tr>
<th>Name</th>
<th>First year</th>
<th>Last year</th>
<th>Length (years)</th>
<th>Trees</th>
<th>Radii</th>
<th>RW (mm)</th>
<th>MS</th>
<th>AR(1)</th>
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<td>Mean</td>
<td>Std</td>
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<tr>
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<td>2008</td>
<td>139</td>
<td>17</td>
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<tr>
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<td>36</td>
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</tr>
<tr>
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<td>18</td>
<td>34</td>
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</tr>
<tr>
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<td>1.253</td>
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**Results**

Climate characteristics and xylem trait interrelationships

Over the past 100 years, there was a mean annual temperature increase of ~3 °C at Tunisian sites and 2 °C at Spanish sites, but no trends in mean annual precipitation (Figure 4). During the last 30 years (coinciding with our vessel data time series), temperatures have increased by 1.5 and 1.0 °C, respectively. Hence, there has been an increase in the overall water stress in recent decades. The annual summer drought period lasts from June to September (Figure 1). Although a few individual trees were older than 350 years (Table 1), the final RW chronologies included only those periods with at least five trees, resulting in chronology lengths between 99 and 181 years (Table 2, see Supplement S1 available as Supplementary Data at Tree Physiology Online). Vessel series had variable intrasite correlations (Table 3) and their mean site chronologies corresponded well along the two altitudinal gradients (Figure 3). Xylem traits were also interrelated. Trees grew more those years with greater DVl (Figure 5c). Dvl increased asymptotically with DVl and RW up to ~3 vessels-mm⁻¹ and 1 mm, respectively (Figure 5b and e). Kvl was linearly related to DVl (Figure 5f) and both expressed an inverse relationship with RW (Figure 5a and d), as expected for the vessel diameter.

**Analyses**

To compare EV characteristics at different altitudes we used linear mixed models, which include fixed and random effects and can take into account the serial correlation contained within individual tree data series of xylem traits (Diggle et al. 2002). The models were of the form: EVl = (μ + a) + βl + εl, with EVl being a specific xylem trait (either RW, MVA, DV, DVl, Dvl or Kvl for the period 1976–2008), μ being the grand mean, βl being an estimated coefficient for each of the n different altitudes within the altitudinal gradients and εl being the random error associated. The final model included a first-order autoregressive moving average [ARMA(1,1)] variance–covariance structure and a random intercept (a) for each tree (random effect), as selected from the most parsimonious formulation using log-likelihood ratio tests. We performed partition of variance in the final models to separate the influence of altitude on EV variability from that of the trees (expressed by the random intercept). To explore relationships between climatic covariates and xylem traits, we used correlation analyses. Climatic data included monthly precipitation, temperature (period 1901–2006) and Palmer drought severity index (PDSI) (period 1901–2002) and were obtained from http://climexp.knmi.nl/get_index.cgi. We calculated a second drought index (HI), by dividing temperature in °C by precipitation in mm (Tuhkanen 1980). Unless otherwise indicated, all significance levels are at α = 0.05.

**Image analysis** (Fonti et al. 2009). After preparation, all vessels with lumen cross-section >10,000 μm² were measured ring by ring. To study xylem functional spatio-temporal variability, we built annual time series of mean vessel area (MVA); a hydraulically weighted diameter (Dvl = Σldl / Σdl², for n vessels of diameter d in year t) proportional to the Hagen–Pousselie (HP) conductivity and thus proportional to xylem hydraulic conductivity (Sperry et al. 1994, Fichot et al. 2009); vessel density (DV in mm⁻³); and linear vessel density (DVl in mm⁻³, calculated as the total number of vessels produced each year divided by the core width). Finally, we calculated the theoretical xylem hydraulic conductivity (kg m⁻¹ s⁻¹ MPa⁻¹) of the ring in year t according to the HP law (Tyree and Zimmermann 2002): Kvl = (ρ / 128η√Amp)∑dia², where ρ is the density of water at 20 °C (998.2 kg m⁻³), η is the viscosity of water at 20 °C (1.002 × 10⁻³ MPa s), √Amp is the area of the image analyzed of the ring in year t and dia is the diameter of each one of the n vessels measured in year t. In ring-porous species, DVl may reflect complementary physiological information compared with DV and RW, because DV of EVs is very closely related to RW. We explicitly avoided juvenile wood, and vessel trait series of the trees sampled did not exhibit any apparent non-climatic trend (Figure 3). Therefore, the EV trait chronologies could be calculated by simply averaging the raw annual time series.
class studied in the case of DV. \( K_H \) was directly related to \( D_H \) and \( D_{Vl} \) (not shown) as could be expected.

### Variation in xylem traits along climatic gradients

During the period when EVs were studied (1975–2008), trees adjusted their xylem traits with altitude. Trees at higher elevations generally exhibited larger \( D_H \), \( D_{Vl} \), \( RW \) and, consequently, smaller \( DV \) than trees at the lowest elevations (Table 3, Figures 3 and 6). \( K_H \) did not vary in average among altitudes (Table 3) but exhibited interannual variability (Figure 3). Trees at the highest altitude in Tunisia presented the greatest \( RW \) and \( D_{Vl} \) (Table 3). However, variability in xylem traits explained by altitude was smaller than that explained by individual variability between trees (Table 4).

We observed no trend in the last 30 years in EVs (Figure 3) as a response to the increase in temperatures observed during the same period (low to medium frequency). Trends in \( RW \) were likely related to periods of abrupt growth release, e.g., during the 1890s and 1930s–1940s in TUN4 (Figure 6, see Supplement S2 available as Supplementary Data at Tree Physiology Online), originated by management rather than climate.

### Spatio-temporal variability in climate signal

Xylem traits responded to short-term (high-frequency) variability in climate. Little correlation was found between MVA and climate, and \( DV_l \) responded to similar climatic variables as \( D_H \) (data not shown). Ring width and vessel anatomical features encoded a partially different climatic signal, with \( RW \) responding more to monthly precipitations and vessel traits responding more to temperatures. Tree growth, i.e., \( RW \), responded positively to precipitation and negatively to temperatures of spring of the current year and fall of the previous year (Figure 7).

Winter climate was in general not significant for growth, except...
Figure 3. Mean annual linear density of vessels (DV, mm⁻¹), density of vessels DV, mm⁻²), hydraulic diameter (DH, mm) and HP conductivity (KH, kg m⁻¹ s⁻¹ MPa⁻¹) for the five sites. Only traits showing significant difference between sites (Table 3) are shown.

Figure 4. Climate chronseries and fitted 20-year splines: (a) and (b) are data from Cadiz whereas (c) and (d) are data from Tunisia. P may, May precipitation; Pannual, annual precipitation; PDSIoct, October Palmer drought severity index; Tmean_annual, mean annual temperature.
that the overall highest response of $D_H$ and also $K_H$ was negative to winter temperatures and positive to early spring (Figures 7 and 8). DV responded similarly to $K_H$ but oppositely to RW, showing positive correlations with temperatures of the current year of growth and negative with precipitations in late spring (Figures 7 and 8). The current year’s summer climate affected significantly mainly EVs (Figure 7 and 8).

All xylem traits responded to drought (Figure 9) but elevation affected the previously described regional response. Trees at lower elevations showed a higher response to all water stress indices, i.e., precipitation, HI and PDSI (Figure 9). The more negative response to increasing water stress at lower elevations was clearer in Southern Spain, where the difference between altitudes was greater. Again, correlations of RW were generally opposite to those of DV and $K_H$. $D_H$ responded to water stress indices from the previous year and spring of the current year.

Discussion

Xylem trait adjustment to climate variability

Our results indicate that *Q. canariensis* modifies its xylem hydraulic system when exposed to dry conditions towards smaller, less numerous EVs but increased vessel density resulting from reduced growth (Martinez-Vilalta et al. 2002, Preston et al. 2006, Cai and Tyree 2010). Hence, these xylem characteristics produced during dry conditions would tend to promote lower whole-plant hydraulic conductance. This strategy may allow trees to conserve soil water and avoid extremely negative water potentials during the dry Mediterranean summers (Hubbard et al. 2001, Mencuccini 2003, Fichot et al. 2009, 2011). In angiosperms vessel density is an indicator of safety and is inversely correlated with the MVA (Poorter et al. 2010, Russo et al. 2010, Zanne et al. 2010). So although we
Figure 6. Mean annual growth as a function of time (calendar year) for Spain (above) and Tunisia (below). Only those trees included in the anatomical analyses were used to calculate the mean trend, which was fitted by cubic smoothing splines with a 50% cut-off of 30 years (thick lines).

Figure 7. Pearson correlation between detrended RW growth indices ($G_{RW}$, period 1901–2006, above), calculated theoretical HP conductivity ($K_{z}$, period 1975–2006, below) and monthly climatic indices. Dashed lines indicate the significance levels. $P$, precipitation, $T_{max}$, maximum temperature, $T_{mean}$, mean temperature.
Figure 8. Pearson correlations (period 1975–2006) between the annual xylem hydraulic diameter ($D_h$) chronologies and monthly climatic variables (above), and between the annual total density of vessels (DV) chronologies and climatic variables (below). Horizontal dashed lines indicate significance levels. P, precipitation; Tmean, mean temperature.

Figure 9. Pearson correlations between detrended RW growth indices ($G_{IRW}$), hydraulic diameter ($D_h$), density of vessels (DV) chronologies and seasonal precipitation and selected drought covariates for the common period 1975–2006 in the two altitudinal gradients. P, precipitation; HI, heat-moisture index; PDSI, Palmer drought severity index; hydro, hydrological year; spring, April–June; fall, October–November. Horizontal dashed lines indicate significance levels.
did not carry out any measurement of actual xylem resistance to cavitation (e.g., Cai and Tyree 2010), our results suggest that larger and more abundant vessels under mesic conditions would allow for more efficient water transport. However, these larger conduits may also promote a greater risk of cavitation during drought (Cochard and Tyree 1990, Hacke and Sperry 2001, Preston et al. 2006).

There is a direct relationship between hydraulic conductance and annual growth performance (Fichot et al. 2009, Russo et al. 2010). In our species, this relationship was achieved by the formation of more and bigger EVs which, however, rely mostly on stored carbohydrates before the growing season (Barbaroux et al. 2003, Hoch et al. 2003). As a response to mesic conditions (Figures 8 and 9), trees enhanced growth coupled to an increase in $D_{v}$ up to a low growth threshold around 1 mm (Figure 5c). Growth $>1$ mm was promoted by production of a larger number of vessels (Figure 5e) but not an increase in vessel frequency as well as $K_{v}$ which can be considered an expression of more reduced xylem efficiency (i.e., less potential conductivity per xylem unit area).

The intensity of trees’ response to climate is affected, among other factors, by climate changing over time (e.g., D’Arrigo et al. 2008). The adjustment of xylem was clear in the response to short-term, annual variability in climatic conditions and also when comparing altitudes. However, results did not suggest clear trends in xylem acclimation to increases in temperatures during the last 30 years. The local most apparent trends observed in growth were likely originated through forest management practices (Aloui and Serre-Bachet 1987, Messaoudene and Tessier 1991, Urbie et al. 2008). At lower elevations we had nevertheless expected long-term modifications of the anatomical characteristics of the vessel network (Tyree and Zimmermann 2002, Mencuccini 2003) and growth (Piovesan et al. 2008, Sarris et al. 2011) to the ongoing changes in climatic conditions. Vessel size and number are considered the primary indicators of vascular strategy, but they cannot fully account for differences in species’ water-conducting patterns and xylem functions (Russo et al. 2010, Umebayashi et al. 2010, Zanne et al. 2010). Hydraulic efficiency is coordinated with other plant functional traits involved in carbon and water relations to maximize productivity (Fichot et al. 2011). So it is possible that trees’ responses to long-term water stress increase were expressed through other physiological mechanisms, at periods longer than 30 years (Q. canariensis can live several hundred years) or that the long-term acclimation of xylem to climate is a non-linear process (Mencuccini 2003) and therefore we cannot describe particular ecological thresholds before they are crossed. Plants adjust their hydraulic system to increasing drought stress in different coordinated ways. They can modify the timing of photosynthesis by avoiding unfavorable conditions; improving access to soil water through changes in the root system; minimizing water consumption by reducing leaf area; increasing the root–shoot ratio; reducing hydraulic tension by modifying the sapwood-transpiring leaf area relation; modifying the vessel frequency; shifting stomatal regulation and stomatal density; and changing water use efficiency with leaf N concentration or leaf area modifications with CO$_2$ enrichment (Breda et al. 2006, Fichot et al. 2009, Limousin et al. 2010).

**Non-climatic factors affecting xylem phenotypic plasticity**

Differences in xylem traits between sites can be partially explained by non-climatic factors, including stand characteristics such as competition and soil, and individual tree features. Stand competition modifies the relationship between growth and climate (Gea-Izquierdo et al. 2009, Martin-Benito et al. 2011) and also should modify how vessel traits of trees respond to climate, which was the case with *Rhododendron* sp. growing under different light intensities (Cordero and Nilsen 2002). High stand densities also reduce individual growth rate and timing, and this is closely related to crown area (Piutti and Cescatti 1997, Misson et al. 2003, Rathgeber et al. 2011). Therefore, the greatest xylem trait values in TUNhigh, were partly explained by the lower stand densities at that site achieved through human management (Ajbilou et al. 2006). Differences between individual oaks explained more variability in vessel traits than differences in elevation (Table 4). Locally, this means that sample size (sensu García-González and Fonti 2008), microsite or genetic imprint (Fichot et al. 2009) could strongly influence the average individual xylem characteristics. Differences between the two regions studied could also express heterogeneous adaptation capabilities of different provenances to dry conditions (Mencuccini 2003, Chen et al. 2010). Some of this variability could explain why our results match the increase in MVA along a precipitation gradient observed in evergreen oaks but not those results in a Mediterranean deciduous oak in northern Spain (Villar-Salvador et al. 1997). We discard the possibility that the observed differences in xylem traits between altitudes were explained by size or age because samples selected for the analyses were rather homogeneous (Table 3).

**Xylem traits reflect climate variability differently**

All the xylem trait chronologies produced were sufficiently robust to analyze how trees responded to climate (Messaoudene and Tessier 1991, Tessier et al. 1994, Fonti et al. 2010). The common signal and sensitivity of vessel chronologies are generally lower than those of RW chronologies (Tardif and Conciatori 2006, Fonti et al. 2010), and different traits show different levels of variability (Fichot et al. 2009). In spite of the close relationships observed between vessel traits and growth, EV traits and absolute annual growth are governed by physiological processes partly occurring on different time scales.
The strong relationship between xylem traits and precipitation and drought indices (Figure 9) likely reflects trees’ capacity to assimilate and allocate carbon during periods when there is lower water stress, similar to other species in Mediterranean ecosystems (Corcuera et al. 2004, Camarero et al. 2010, Vaz et al. 2010, Gea-Izquierdo et al. 2011). $D_u$ and $K_u$ of Q. canariensis reflected the climate in winter and early spring before and during EV formation, similar to other ring-porous deciduous species (García-González and Eckstein 2003, Fonti and García-González 2004, Tardif and Concariori 2006, Voelker et al. 2012). This negative relationship with winter temperatures could be due to high respiration rates and consumption of stored carbohydrates in winter when trees hold no leaves or photosynthetic rates are low (Fonti and García-González 2004). Oak $K_u$ and DV showed positive correlations with temperatures from spring to early fall, which for $D_u$ were only positive in early spring. Nevertheless, these positive correlations were not equally present at all sites, which is different from results by Voelker et al. (2012), who found a coherent spring temperature signal in earlywood traits across a species range. The response to temperature was much clearer in vessel traits than in growth. However, the positive response of $K_u$ and DV to temperatures just mentioned should be indirectly reflecting (apparently, better than RW) the influence of climate on latewood growth, hence higher climatic constraints for trees during the growing season. The overall regional response to climate reflected by xylem traits was modified by local climatic conditions at different altitudes. Trees at low elevations responded more to cumulative water availability and drought indices (Figure 9), which is in agreement with the variability in xylem traits (Table 3) discussed in the previous section. These changes reflect the shifts in growing season usually occurring along elevation gradients (Aloui and Serre-Bacht 1987, Gordo and Sanz 2009, Voelker et al. 2012) and suggest that trees at low elevations suffer more from the overall water stress.

In Mediterranean ecosystems, most plant species are adapted to favorable conditions in spring and fall. Trees reduce their gas exchange during dry summers, and generally exhibit higher net photosynthetic rates again in fall (Baldocchi et al. 2010, Vaz et al. 2010). These adjustments allow Mediterranean trees of different functional types to continue to grow in fall, although evergreens seem to benefit more from appropriate climatic conditions in fall than deciduous species (Montserrat-Martí et al. 2009, Camarero et al. 2010, Gutiérrez et al. 2011). A positive response of conductivity to the previous year’s fall climate has been observed in evergreen Mediterranean oaks (Corcuera et al. 2004) but not in temperate deciduous species (García-González and Eckstein 2003, Fonti and Garcia-González 2004). There are no cambial phenology data for Q. canariensis but observed correlations between the xylem traits and climate in early fall suggest that this facultative deciduous species can also grow in fall.

Conclusions

This comparative study of xylem trait variability across series of tree rings shows how facultative deciduous Q. canariensis trees growing in summer water-stressed environments adjust their xylem hydraulic characteristics to fit environmental constraints. The xylem traits showed high phenotypic plasticity. The correlations between xylem traits and climate and the observed differences among altitudes suggest that the trees respond to more water availability by increasing growth coupled to an increase in the vessel diameters up to a threshold after which they increase absolute hydraulic conductance by increasing the number of big vessels. Growth was inversely related to potential conductivity per xylem unit area and during dry and warm years trees produced xylems with higher vessel density and likely a safer and more efficient (greater potential conductivity per xylem area) hydraulic architecture. These adjustments mostly reflected annual short-term variability in climate and local differences in overall water stress within altitudinal gradients. We observed no clear long-term (30 years) response to temperature increase in the xylem traits. Nevertheless, based on the observed responses to climate, we believe that the additional increase in water stress predicted by future climate scenarios could negatively influence Q. canariensis performance at local low elevation limits where the species is currently present. These results show that functional relationships between xylem traits exhibit both spatial and temporal plasticity in relation to climatic variability. Therefore, it would be desirable that studies analyzing functional relationships in xylem architecture include multiple time scales.

Supplementary data

Supplementary data for this article are available at Tree Physiology online.

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Conflict of interest
None declared.

References


