

Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought

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Summary In the Mediterranean evergreen oak woodlands of southern Portugal, the main tree species are *Quercus ilex* ssp. *rotundifolia* Lam. (holm oak) and *Quercus suber* L. (cork oak). We studied a savannah-type woodland where these species co-exist, with the aim of better understanding the mechanisms of tree adaptation to seasonal drought. In both species, seasonal variations in transpiration and predawn leaf water potential showed a maximum in spring followed by a decline through the rainless summer and a recovery with autumn rainfall. Although the observed decrease in predawn leaf water potential in summer indicates soil water depletion, trees maintained transpiration rates above 0.7 mm day^{-1} during the summer drought. By that time, more than 70% of the transpired water was being taken from groundwater sources. The daily fluctuations in soil water content suggest that some root uptake of groundwater was mediated through the upper soil layers by hydraulic lift. During the dry season, *Q. ilex* maintained higher predawn leaf water potentials, canopy conductances and transpiration rates than *Q. suber*. The higher water status of *Q. ilex* was likely associated with their deeper root systems compared with *Q. suber*. Whole-tree hydraulic conductance and minimum midday leaf water potential were lower in *Q. ilex*, indicating that *Q. ilex* was more tolerant to drought than *Q. suber*. Overall, *Q. ilex* seemed to have more effective drought avoidance and drought tolerance mechanisms than *Q. suber*.

Keywords: canopy conductance, groundwater, hydraulic conductance, leaf water potential, *Quercus ilex*, *Quercus suber*, sap flow.

Introduction

Mediterranean-type evergreen oak woodlands cover substantial areas in the world. In the Iberian Peninsula, they occupy an area of about 2–2.5 million ha. In western Iberia, anthropogenic factors have shaped these oak woodlands into savannah-type ecosystems. These ecosystems are subject to silvo-

pastoral exploitation, and there is a concern about their sustainability. Droughts are considered the main cause of enhanced tree mortality in these oak woodlands (David et al. 1992). In a strongly seasonal climate, the long-term sustainability of these ecosystems may be further threatened by the regional effects of global warming, which are predicted to result in increases in the length, severity and frequency of summer droughts (Miranda et al. 2002).

In southern Portugal (Alentejo province), the main tree species are *Quercus ilex* ssp. *rotundifolia* Lam. (holm oak) and *Quercus suber* L. (cork oak). They are managed mainly for the production of acorns to feed livestock and cork, respectively. Although both species often coexist, *Q. ilex* is mainly concentrated in the drier, eastern inland regions, whereas *Q. suber* dominates in the wetter, western coastal areas. Though influenced by human activity, this geographical distribution suggests that *Q. ilex* is better adapted to limited water availability than *Q. suber*. Therefore, it may be expected that, compared with *Q. suber*, the abundance and distribution of *Q. ilex* will be less affected by the predicted increase in the severity of summer droughts caused by climate change.

There have been many studies on the responses of *Q. ilex* to drought (e.g., Infante et al. 1997, Tognetti et al. 1998, Martínez-Vilalta et al. 2002, Infante et al. 2003, David et al. 2004), but there are few reports on the drought responses of *Q. suber* (Oliveira et al. 1992, Nardini and Tyree 1999, Kurz-Besson et al. 2006), and only two studies have made a direct comparison of the drought tolerance features of *Q. ilex* and *Q. suber* (Tyree and Cochard 1996, Mediavilla and Escudero 2003). What is known is that *Q. ilex* and *Q. suber* display stomatal control over transpiration during the summer drought (Mediavilla and Escudero 2003) and have access to both soil and groundwater (David et al. 2004, Lubczynski and Gurwin 2005, Kurz-Besson et al. 2006), and that *Q. ilex* is more resistant to xylem embolism than *Q. suber* (Tyree and Cochard 1996).

To our knowledge, there are no published studies on the long-term responses of *Q. ilex* and *Q. suber* under similar field

conditions. To gain insight into the likely adaptations of these evergreen oaks to anticipated climate change, we undertook a comparative study of *Q. ilex* and *Q. suber* in a mixed species woodland (*montado*). Specific objectives were to characterize the seasonal patterns of transpiration and sources of water supply to roots and to determine how water use is controlled. We hypothesized that: (1) *Q. ilex* exhibits more conservative water use than *Q. suber*; (2) *Q. ilex* has better access to deep water than *Q. suber*; and (3) hydraulic properties of the root–leaf flow path underlie possible differences in drought resistance between the species.

Material and methods

Experimental site

The experiment was conducted, between 2001 and 2003, in a mixed *montado* located at Herdade da Alfarrobeira (38°32'26" N, 8°00'01" W, 220–250 m a.s.l.), near Évora in southern Portugal. Tree cover consists mainly of sparse holm oak trees with scattered patches of cork oak. Mean stand density and tree crown cover are about 30 trees ha⁻¹ and 21%, respectively (Carreiras et al. 2006). The understory consists of natural pasture of herbaceous annuals (e.g., gramineae such as *Vulpia bromoides* (L.) S.F. Gray and *Avena barbata* Link and legumes such as *Ornithopus compressus* L. and *Trifolium subterraneum* L.) invaded by shrubs, mainly *Cistus salviifolius* L.

The climate is Mediterranean, with dry hot summers and rainy mild winters. Long-term (1951–1980) mean annual rainfall is 665 mm, mainly concentrated from autumn to early spring (90%) in less than 75 days of rain per year (INMG 1991). Mean annual open water evaporation is 1760 mm, and mean annual air temperature is about 15 °C, ranging from 8.6 °C in January to 23.1 °C in August (INMG 1991). The soil is a Dystric Cambisol (FAO 1988), with a maximum soil depth of around 1 m and a low water retention capacity, overlying granite bedrock.

Plant material

Three cork oak and four holm oak trees were selected in adjacent plots (about 150 m apart). Trunk diameter at breast height, crown projected area and height of the sampled trees ranged from 0.45 to 0.53 m, 91.13 to 150.19 m² and 8.5 to 9.5 m in *Q. suber* and 0.33 to 0.43 m, 47.71 to 89.99 m² and 7 to 8 m in *Q. ilex*, respectively. Mean diameter at breast height (DBH) of cork and holm oak was 0.42 (± 0.18) and 0.34 (± 0.17) m, respectively.

Tree leaf area index (*L*) was not measured at the site. However, *L* was estimated by destructive sampling in spring of two *Q. suber* and two *Q. ilex* trees in another research project in the vicinity of our experimental area. Estimated mean *L* for *Q. suber* and *Q. ilex* was 3 and 3.4 per unit of crown-projected area, respectively (unpublished data).

Meteorological data

An automated weather station was mounted on top of a 25-m-

high tower (about 17 m above mean canopy height). Solar radiation (CM6B, Kipp and Zonen, Delft, The Netherlands), dry and wet bulb temperatures (aspirated psychrometer H301, Vector Instruments, Rhyl, U.K.), wind direction (wind vane W200P, Vector Instruments, Rhyl, U.K.), wind velocity (anemometer A100R, Vector Instruments) and rainfall (tipping-bucket rain gauge ARG100, Environmental Measurements, Gateshead, U.K.) were recorded as 10-min means or totals with a CR10X data logger (Campbell Scientific, Shepshed, U.K.). Air vapor pressure deficit was calculated from dry and wet bulb temperatures.

Groundwater table

Fluctuations in groundwater level were monitored in two 20-m-deep boreholes at each of the plots. The boreholes were dug in late 2001. Water table depth was monitored during 2002 and 2003 by pressure transducers (PDCR 830, Campbell Scientific) and recorded at 10-min intervals by CR10X data loggers, which measure the difference in pressure between the atmosphere and that at the depth of the sensor.

Sap flow

Sap flow was continuously measured in the sampled *Q. ilex* and *Q. suber* trees by the Granier method (Granier 1985, 1987) from January 2001 to December 2003. One sensor (UP GmbH, Landshut, Germany) was inserted radially in the south-facing xylem of each tree. Each sensor consists of a pair of 20-mm-long probes inserted in the tree stem at breast height, and 15 cm apart vertically. The upper probe was heated by a constant current, whereas the lower probe was unheated and remained at trunk temperature. Sensors were connected to CR10X data loggers, scanning temperature differences between probes (ΔT) every 10 s and recording 10-min means. Sap flux density was calculated from 10-min values and the absolute maximum temperature difference between probes (ΔT_{\max}) over 10-day periods (see Granier (1985) for further details). Sap flow sensors were replaced only in case of disruption, since it has been shown that probes do not deteriorate with time and are reliable for long-term measurements in these oak species (David et al. 2004). Sapwood conductive thickness was estimated from the sap flow radial profile obtained by the heat field deformation method (Nadezhdina et al. 1998) in one *Q. suber* and two *Q. ilex* trees. Results showed that only the outer 30 and 32% of the trunk radius was conductive in *Q. ilex* and *Q. suber*, respectively. In the absence of additional measurements, these percentage values were used to estimate the effective sapwood depth of the remaining sampled trees of each species. Estimated hydroactive xylem thickness in the studied individuals ranged from 5 to 8.5 cm, which always exceeded the Granier probe length. Tree sap flow (*F*) was calculated as the product of sap flow density (measured by the Granier probes) and the sapwood conductive area of each tree. This simplified approach yields accurate results only when the radial profile of sap flux density is uniform or when the sap flux density measured by the sensor is a good estimate of the average sap flux density over the entire conductive sapwood area. When neither of these conditions is met, large errors can

result unless the variation in the radial profile of sap flow is taken into account (James et al. 2002, Nadezhdina et al. 2002). Because only one sensor was installed per tree, additional errors may have arisen from neglecting circumferential sap flux variability (James et al. 2002). Because the assumption of evenly distributed sap flux density is frequently made (e.g., Martínez-Vilalta et al. 2003, Bucci et al. 2004a) and because the sampling and calculation procedures were the same in all trees, any errors will tend to have been systematic and should not affect our comparative analyses of the relative variation in tree sap flow in time or between species (Martínez-Vilalta et al. 2003).

Several additional facts concur to suggest that our simplified method may provide not only reliable comparative evaluations, but also reasonably accurate absolute results. First, David et al. (2004) found that 20-mm Granier sensors provided a good estimate of the mean sap flux density over the entire conductive sapwood area of a *Q. ilex* tree, even though the radial sap flow distribution was non-uniform. These authors measured the radial sap flow profile with multiple-point heat pulse sensors (Cohen 1994). Although these comparative tests were made only in *Q. ilex*, we think that it is acceptable to generalize them to *Q. suber*, given the similarity in sapwood anatomy of these species (Leal et al. 2006). Second, both studied oak species are diffuse-porous (e.g., Corcuera et al. 2004), and Clearwater et al. (1999) reported that the radial distribution of sap flux density is usually more even (uniform or Gaussian) in diffuse-porous than in ring-porous species. Finally, our tree sap flow estimates were recently checked against eddy covariance water vapor flux data, with encouraging results. During the Mediterranean dry summer, understory transpiration is negligible, and tree transpiration can be considered the sole component of ecosystem evapotranspiration. When our estimates of F were scaled up to the ecosystem level (considering tree canopy cover), the agreement between the F and eddy covariance data was good throughout the summer drought of 2005 (unpublished data). Overall, we believe that the procedures we adopted and the resulting sap flow data are adequate for comparative analyses, and may be appropriate for estimating absolute whole-tree water use.

Tree transpiration (E) was considered equal to F when steady-state conditions prevailed (daily totals and midday values). Sap flow rates and leaf water potentials (Ψ_l) were usually remarkably constant for about 4 h around midday solar time on days with clear skies, indicating the prevalence of steady-state conditions at that time (cf. David et al. 2004). Both E and F were expressed per unit of crown-projected area ($\text{kg m}^{-2} \text{s}^{-1}$ or mm day^{-1} or mm h^{-1}).

Leaf water potential

Tree water status was assessed by measuring Ψ_l on a monthly basis from January 2002 to November 2003, with a Scholander pressure chamber (PMS 1000, PMS Instruments, Corvallis, OR) (Scholander et al. 1965). Scaffold towers allowed direct access to the south-facing part of the crowns of the studied trees. Three to four leaves were sampled in each tree just before sunrise (predawn leaf water potential, $\Psi_{l, \text{pd}}$)

and around midday solar time (midday leaf water potential, $\Psi_{l, \text{md}}$). Samples were taken at similar heights aboveground to avoid variability caused by hydrostatic water potential and immediately placed in a plastic bag to prevent further transpiration.

It is frequently assumed that Ψ_l is in equilibrium with soil water potential (Ψ_s) before dawn, permitting the use of $\Psi_{l, \text{pd}}$ as a surrogate for Ψ_s (e.g., Crombie et al. 1988, Richter 1997). However, if processes such as nighttime transpiration prevent equilibrium, the assumption may be invalid (Bucci et al. 2004b). To test for equilibration at the end of the night, $\Psi_{l, \text{pd}}$ was also measured on three summers days (one in 2002 and two in 2003) on leaves that had been covered with aluminum-foil-coated bags since the previous evening (three covered leaves per tree). On all the sampling days $\Psi_{l, \text{pd}}$ values were identical in covered and uncovered leaves, suggesting that $\Psi_{l, \text{pd}}$ was in equilibrium with Ψ_s by the end of the night. Additionally, sap flow data showed no significant nocturnal transpiration during most of the study, except for rare short periods when nighttime vapor pressure deficit was high. Therefore, $\Psi_{l, \text{pd}}$ was assumed to provide an adequate estimate of Ψ_s near the tree roots.

Whole-plant hydraulic conductance

Water transport in the pathway from soil or groundwater to leaves can be described according to Darcy's law (Wullschlegel et al. 1998, Sperry 2000):

$$F = k(\Psi_s - \Psi_l) \quad (1)$$

where F is in $\text{kg m}^{-2} \text{s}^{-1}$, k is total hydraulic conductance from roots to leaves ($\text{kg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) and Ψ_s and Ψ_l are in MPa. The difference between $\Psi_{l, \text{pd}}$ and $\Psi_{l, \text{md}}$ is an estimate of the sap flow driving force ($\Psi_s - \Psi_l$) at midday, because $\Psi_{l, \text{pd}}$ is considered equal to Ψ_s . Whole-tree hydraulic conductance was estimated from measurements of midday sap flow (F_{md}), $\Psi_{l, \text{md}}$ and $\Psi_{l, \text{pd}}$, as the only unknown of Equation 1. Calculations were performed for springs and summers of 2002 and 2003 and averaged for the *Q. ilex* and *Q. suber* samples. Hydraulic conductance was expressed relative to the crown-projected area.

Canopy conductance

Given the high degree of coupling between the atmosphere and the canopy in these evergreen oak woodlands (low decoupling coefficients at the leaf and tree level (Infante et al. 1997)), E ($\text{kg m}^{-2} \text{s}^{-1}$) can be approximated by (McNaughton and Jarvis 1983, Jarvis and McNaughton 1986):

$$E = g_c D_e \frac{\rho c_p}{\lambda \gamma} \quad (2)$$

where g_c is canopy conductance (m s^{-1}), mainly dependent on mean leaf stomatal conductance (g_s) and leaf area index (L), D_e is the vapor pressure deficit of the air (Pa), λ is latent heat of evaporation of water (J kg^{-1}), γ is the psychrometric constant ($\text{Pa } ^\circ\text{C}^{-1}$), ρ is the density of air (kg m^{-3}) and c_p is the heat ca-

capacity of water in air ($\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$). Midday canopy conductance ($g_{c,\text{md}}$) was estimated for individual sampled trees from F_{md} and D_e data, as the only unknown of Equation 2. Midday values were hourly means centered on midday solar time. Calculations were performed for springs and summers of 2002 and 2003 and averaged for the *Q. ilex* and *Q. suber* samples. Canopy conductance values were expressed relative to crown-projected area.

Sensitivity of the response of g_c (mm s^{-1}) to D_e (kPa) was determined by fitting the following equation to the data (Oren et al. 1999):

$$g_c = b - m \ln D_e \quad (3)$$

where the slope of the line is $dg_c/d\ln D_e = -m$, and b is the intercept. The parameter m quantifies the sensitivity of g_c to D_e and b is a reference conductance ($b = g_{c,\text{ref}}$) at $D_e = 1$ kPa.

Soil water content

Soil profiles were sampled under the canopy edge of three to four trees of each oak species in mid-June (late spring) and mid-August (summer) 2002. Samples were collected every 0.2 m from the surface down to a depth of 1 m. Soil volumetric water content (SWC) was measured by the gravimetric method.

During the summer of 2003, short-term variations in SWC were monitored by ThetaProbe sensors (ML2x, Delta-T Devices, Cambridge, U.K.) connected to a DL2e data-logger (Delta-T Devices). Four sensors were installed in the soil, following a north-facing radial layout, at different distances from the trunk (1, 3, 4 and 6 m) of one of the studied *Q. ilex* trees. The outer sensor was outside the crown projection limits: crown radius was 4.2 m. All sensors were installed at a 0.35-m depth, where most of the shallow roots were found. Before installation of the sensors, shrubs and grasses were cut under and beyond the tree canopy and soil surface remained free of understory vegetation during the measuring period (summer 2003). Soil volumetric water content data were averaged and stored at half-hourly intervals.

Xylem, soil and groundwater stable hydrogen isotopic composition

Quercus ilex and *Q. suber* water uptake sources were determined by comparing the $^2\text{H}/^1\text{H}$ isotope ratio (δD) of twig xylem water (δD_{xy}) with that of soil water (δD_{sw}) and groundwater (δD_{gw}) in summer (mid-August) 2002. One lignified twig was sampled at midday in four trees of each oak species at a distance of 10 cm from the nearest leaves. All leaves and green stem tissue were removed from woody twigs to avoid contamination of the remaining xylem water by isotopically enriched water (Dawson and Ehleringer 1993). Soil water samples were collected every 0.2 m to a depth of 1 m. Groundwater samples from the two boreholes were collected in plastic test tubes closed with plastic stoppers. All samples for stable isotope analyses were taken in mid-August 2002. Every sample was hermetically sealed with parafilm to avoid any alteration of the isotopic signature as a result of evaporation and kept in the

freezer ($-18 \text{ } ^\circ\text{C}$) until water extraction (by cryodistillation in soil and twig samples) and analysis by mass spectrometry. A 0.7- μl aliquot of the water sample was injected with an autosampler (CombiPal, CTC Analytics, Switzerland) into a high temperature pyrolysis oven (TC/EA, Finnigan, Bremen, Germany), where the water was dissociated at a temperature of $1450 \text{ } ^\circ\text{C}$ into CO and H_2 . The δD of the H_2 was analyzed with an isotope ratio mass spectrometer (IRMS) Delta Plus XL (Finnigan). The value of δD was determined from the time integrals of the peak areas of the ^2H and ^1H ion intensities (m/z 3 and 2) and referenced to the international Vienna Standard Mean Ocean Water (VSMOW). For more details, see Gehre et al. (2004). Values of δD were expressed in parts per thousand (‰) and defined as:

$$\delta D = \frac{R_{\text{sam}} - R_{\text{std}}}{R_{\text{std}}} 1000 \quad (4)$$

where R_{sam} and R_{std} are the δD values of the sample and of the standard, respectively.

Assuming that groundwater and soil water are the only sources of water uptake that might explain xylem twig isotopic composition, a two-component tracer mass balance was used to estimate the water source contribution to tree transpiration (adapted from Dawson 1993):

$$\delta D_{\text{xy}} = A \delta D_{\text{sw}} + (1 - A) \delta D_{\text{gw}} \quad (5)$$

where A and $(1 - A)$ are the contributions of soil and groundwater to xylem water, respectively.

Statistical analyses

Differences in E , $\Psi_{\text{l,pd}}$, $\Psi_{\text{l,md}}$ and k between the two oak species were tested by one-tail Student t -tests. Before each test with independent samples, the hypothesis of equal variance in the sampled populations was evaluated with an F test. When the hypothesis was rejected, the t -test was performed using the Welch modification to calculate the degrees of freedom (Zar 1999). This latter modification was necessary only for the analyses of k and of transpiration in some days.

The effect of time on the mean k value for each oak species (four periods were compared: springs and summers of 2002 and 2003) was evaluated by a single-classification analysis of variance (ANOVA). A Bartlett test performed before each ANOVA confirmed the assumption of homogeneity of variances. Details about the performed tests can be found in standard statistics textbooks (e.g., Montgomery 2004). All statistical analyses were done with R software (R Development Core Team 2005, Vienna, Austria; URL <http://www.R-project.org>).

Results

Seasonal variation in tree transpiration

During the 3-year study, cumulative rainfall exceeded the long-term mean (+19%), although the springs of 2002 and 2003 were drier than average. Rainfall was always scarce dur-

ing the summer, from June to the second half of September (Figure 1a). Water table depth varied between 1.5 and 2 m in mid-spring, at the end of the rainy period, and 5 m in late summer (Figure 1b). Differences in the water table depth between the *Q. ilex* and *Q. suber* plots were negligible.

Seasonal patterns of E were similar for both species (Figure 1c). Daily E peaked in late spring when evaporative demand was high and there were no restrictions on soil water availability. Thereafter, a progressive decline in E was observed, as soil and groundwater became limiting, with the lowest values of E at the end of the dry season (September), followed by a recovery following autumn rains. *Quercus suber* had higher transpiration rates throughout most of the year, except at the end of the summer drought when E was higher in *Q. ilex* (Figures 1c and 2). Differences in mean daily E between *Q. suber* and *Q. ilex* were analyzed for two periods: late spring, when E peaked (May 15 to the end of June) and late summer, when E was lowest (31 days before the onset of autumn rains), for the three study years (2001–2003). Mean E was always higher in *Q. suber* than in *Q. ilex* in late spring, and the difference between species was significant on 47% of the measurement days ($P < 0.05$). In late summer, the opposite pattern occurred: E was higher in *Q. ilex* than in *Q. suber*, and the difference between species was significant on 46% of the

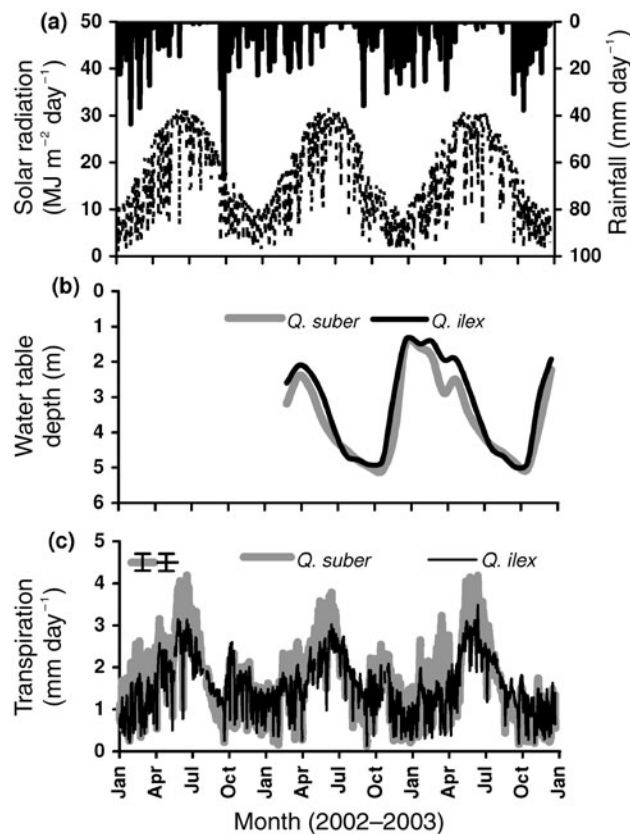


Figure 1. Seasonal variations of daily (a) rainfall and solar radiation, (b) water table depth, and (c) transpiration in *Quercus ilex* and *Q. suber* (2001–2003). In (c), error bars are standard errors of the mean.

measurement days ($P < 0.05$). In spring, maximum daily E was 3.8–4.1 mm in *Q. suber* and 3.0–3.5 mm in *Q. ilex*. By the end of the summer drought, daily E was 1.0–1.2 mm in *Q. ilex* and 0.7–0.8 mm in *Q. suber*. From spring to late summer, water stress reduced E by 79–83% in *Q. suber* and by 60–70% in *Q. ilex*.

Seasonal patterns in leaf water potential

Predawn leaf water potential remained high and approximately constant throughout the wet period (between -0.1 and -0.3 MPa) and declined during the summer drought (Figure 3). Differences in $\Psi_{l,pd}$ between species were particularly marked in late summer (September), when $\Psi_{l,pd}$ remained higher in *Q. ilex* (-1.7 MPa) than in *Q. suber* (-2.3 and -2.1 MPa in 2002 and 2003, respectively). At the end of the summer drought, the differences in $\Psi_{l,pd}$ between species were statistically significant ($P < 0.0001$). Seasonal variations in $\Psi_{l,md}$ were not in phase with the variations in $\Psi_{l,pd}$, being more closely associated with atmospheric conditions than with the progression of drought. During the study, minimum values of $\Psi_{l,md}$ occurred in September 2002 and were -3.48 MPa for *Q. ilex* and -3.0 MPa for *Q. suber*, with the differences between species being statistically significant at $P < 0.0001$.

The seasonal variation in sap flow driving force ($\Psi_{l,pd} - \Psi_{l,md}$) during 2002–2003 was highest during the wet period and declined during the summer drought (Figure 4). The lower sap flow driving forces during summer were caused by reductions in $\Psi_{l,pd}$. Sap flow driving force in late summer (September) was higher in *Q. ilex* than in *Q. suber* (Figure 4), as a result of higher $\Psi_{l,pd}$ (Figure 3). During the wet period, the sap flow driving force did not differ between species. During this period, occasional decreases in the sap flow driving force were associated with the higher $\Psi_{l,md}$ values during cloudy wet days.

Seasonal variation in whole-tree hydraulic conductance

Figure 5 shows the seasonal variation in k for *Q. ilex* and *Q. suber* during the springs (May–June) and summers (August–September) of 2002 and 2003. A single-classification

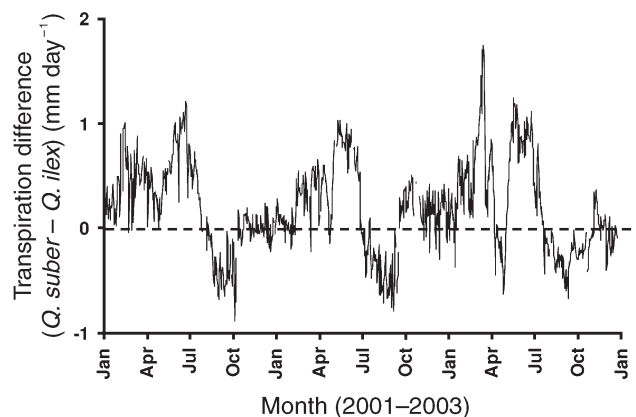


Figure 2. Seasonal variation of the difference between daily transpiration of *Quercus suber* and *Q. ilex* (2001–2003).

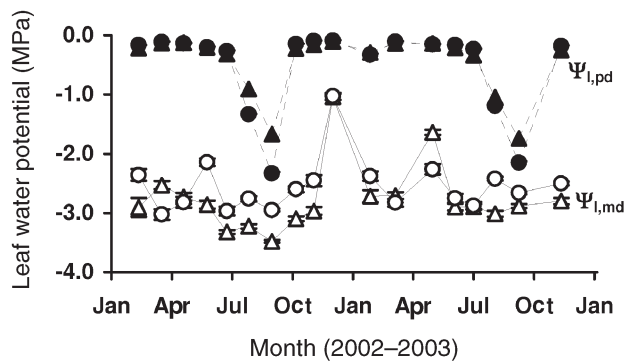


Figure 3. Seasonal variations of predawn (closed symbols) and midday (open symbols) leaf water potential in *Quercus ilex* (▲, △) and *Q. suber* (●, ○) (2002–2003). Error bars are standard errors.

analysis of variance indicated that k did not vary significantly with time (season or year) in either species ($P > 0.25$, for both species). However, k differed significantly between species, being higher in *Q. suber* than in *Q. ilex* (3.15×10^{-5} versus $2.28 \times 10^{-5} \text{ kg m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$; $P < 0.0001$).

Seasonal variation in canopy conductance

Figure 6 shows the relationships between $g_{c,mq}$ and D_e for two periods, representing pre-drought (May–June) and drought conditions (September) for the three years of observations (2001–2003). At a given D_e , g_c was higher in spring and lower during the summer drought, irrespective of species. In the spring, g_c was higher in *Q. suber* than in *Q. ilex*, and the opposite was the case during the summer drought.

Parameter values of the linear regressions between g_c and $\ln D_e$ (Equation 3) are shown in Table 1 for both species and for pre-drought and drought conditions. The relationships between variables were generally strong (minimum $r^2 = 0.82$). Sensitivity of the g_c response to D_e (m) and reference g_c at $D_e = 1 \text{ kPa}$ (b) decreased in both species as the drought progressed. Nevertheless, the ratio $m/b = (-dg_c/d\ln D_e)/g_{c,ref}$ was always close to 0.6, irrespective of species or season.

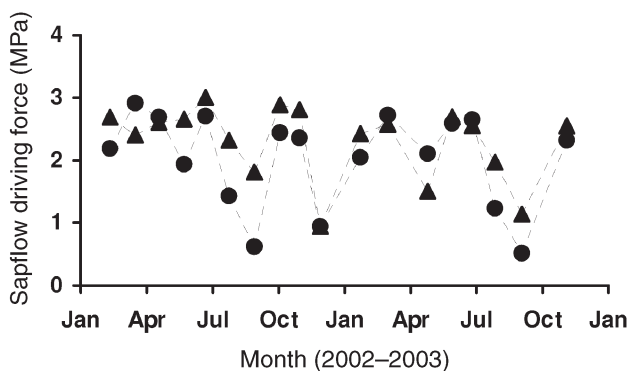


Figure 4. Seasonal variations of sap flow driving force in *Quercus ilex* (▲) and *Q. suber* (●) (2002–2003).

Sources of water for tree roots: soil water and groundwater

Figure 7 shows the soil water profiles under *Q. ilex* and *Q. suber* in mid-June (when transpiration peaked) and in mid-August 2002 (when summer E was reduced) (see Figure 1). From June to August 2002, there was a decrease in soil water content irrespective of the species, mainly below 0.3-m-depth (Figure 7). In August 2002, when soil water content was low and almost constant over the entire soil profile, δD_{xy1} values of both species were compared with those of soil water and groundwater. The δD_{xy1} (\pm SE) of the two species (-32.52 ± 1.59 and $-32.74 \pm 1.31\%$ for *Q. ilex* and *Q. suber*, respectively) were intermediate between that of soil (average over depths of 0.3 to 0.7 m = $-42.83 \pm 0.94\%$) and groundwater ($-28.81 \pm 0.07\%$), indicating that trees were using water from both sources. Soil water values were quite constant over the entire soil profile around the mean value, except for the top 20-cm layer where it was less negative ($-19.9\% \pm 8.2$). The relative contributions of the main water sources (soil and groundwater) to *Q. ilex* and *Q. suber* transpiration, estimated by Equation 5, indicate that most of the water taken up by trees of both species in August 2002 was from groundwater (74 and 72% for *Q. ilex* and *Q. suber*, respectively). At that time there were no differences in the patterns of water uptake between species.

Although soil water content was low over the entire soil profile during the summer (Figure 7), typical diurnal fluctuations were observed at 0.35-m-depth under *Q. ilex* during late summer (September) 2003 (Figure 8). Soil water content increased from about midnight to midday and decreased from noon to the end of the day (Figure 8). These fluctuations occurred at different distances from the *Q. ilex* tree trunk (1, 3, 4 and 6 m), but the amplitude was smaller near the stem (1 m) (Figure 8). We ascribed these fluctuations to hydraulic lift, i.e., water movement from deep to shallow roots at night when the surface soil is dry. Similar measurements were not undertaken under *Q. suber* because of a lack of equipment.

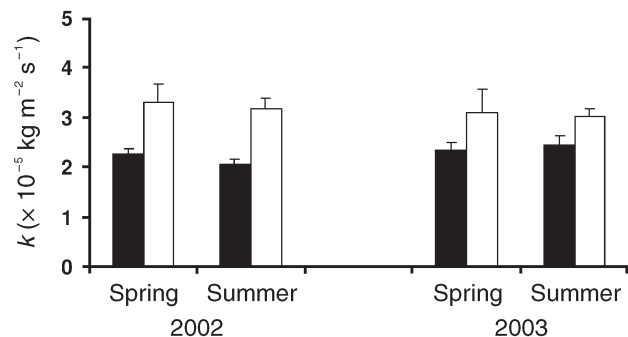


Figure 5. Seasonal variations of spring and summer whole-tree hydraulic conductance (k) in *Quercus ilex* (closed bar) and *Q. suber* (open bar) (2002–2003). Error bars are standard errors.

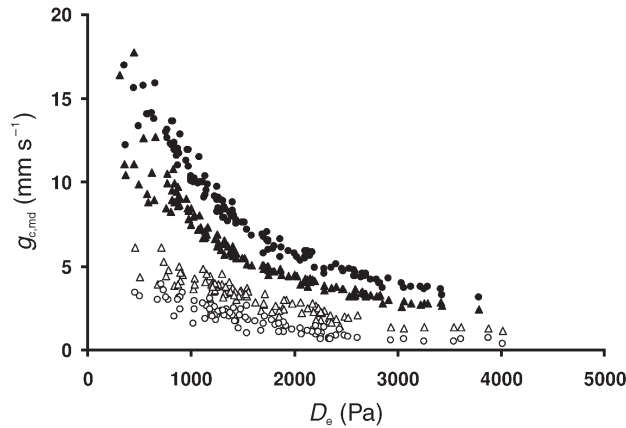


Figure 6. Relationships between midday canopy conductance ($g_{c,md}$) and vapor pressure deficit (D_e) for *Quercus ilex* ($\blacktriangle, \triangle$) and *Q. suber* (\bullet, \circ) for pre-drought (closed symbols) and drought conditions (open symbols) (2001–2003).

Discussion

Seasonal patterns of tree transpiration: the role of groundwater uptake

In both species, seasonal variations in E and $\Psi_{l,pd}$ showed a typical pattern with maximum values in spring followed by a progressive decline during the summer drought and a recovery in response to autumn rains (Figures 1 and 3). The decrease in $\Psi_{l,pd}$ in summer (Figure 3) resulted from decreases in soil water content (Figure 7) and groundwater level (Figure 1). As a consequence, sap flow driving force (Figure 4), g_c (Figure 6) and E (Figure 1) also decreased during the summer. Nevertheless, E continued during the entire drought period at rates that were always above 0.7 mm day^{-1} . During the summer drought, when there was no rainfall, the groundwater table level was about 4–5 m below the soil surface and the soil water content was low (Figures 1 and 7), transpiration was mainly supplied by direct groundwater and subsoil water uptake through deep roots. At that time, more than 70% of the transpired water was from groundwater sources. Several studies have shown that evergreen trees in climates with seasonal drought rely on deep roots and the ability to tap water from sources in the subsoil including permanent water tables (Walter 1973, Breman and Kessler 1995, Canadell et al. 1996). At the global scale, tree rooting depth is greater in drier environments with seasonal

Table 1. Values of the estimated parameters in Equation 3 and their ratio.

Species	Condition	m	b	m/b
<i>Q. ilex</i>	Pre-drought	4.9	7.9	0.62
	Drought	2.4	4.1	0.59
<i>Q. suber</i>	Pre-drought	6.7	10.7	0.63
	Drought	1.7	2.6	0.65

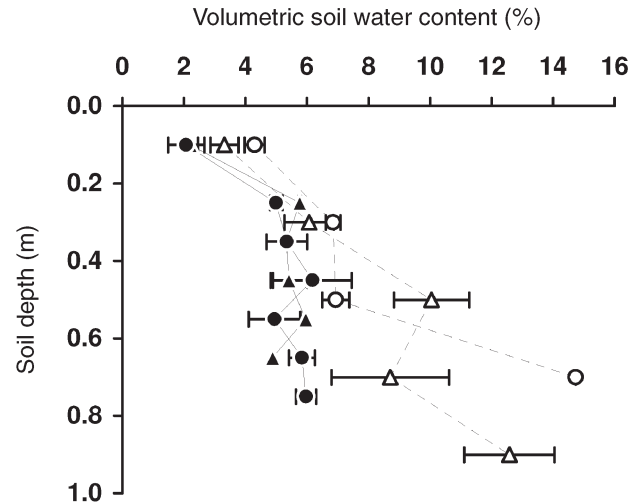


Figure 7. Soil water profiles under *Q. ilex* ($\blacktriangle, \triangle$) and *Q. suber* (\bullet, \circ) in mid-June (open symbols) and mid-August (closed symbols) of 2002. Error bars are standard errors.

drought (Canadell et al. 1996, Schenk and Jackson 2005). Typical maximum rooting depth of sclerophyllous Mediterranean trees (mainly *Eucalyptus* and *Quercus* spp.) is about 13 m (Canadell et al. 1996).

Groundwater uptake by deep roots of *Quercus* spp. can be even more effective than observed at our site, preventing plant water stress or reduced transpiration during the summer drought. For example, David et al. (2004), who studied a *Q. ilex* tree located 3 km away from our site, found that deep rooting was facilitated by the fractured nature of the rock (gneiss), even though the water table was deeper (13 m) than in our experiment (5 m). The finding that evergreen oak trees in Mediterranean woodlands often rely on groundwater was recently confirmed by Lubczynski and Gurwin (2005), who

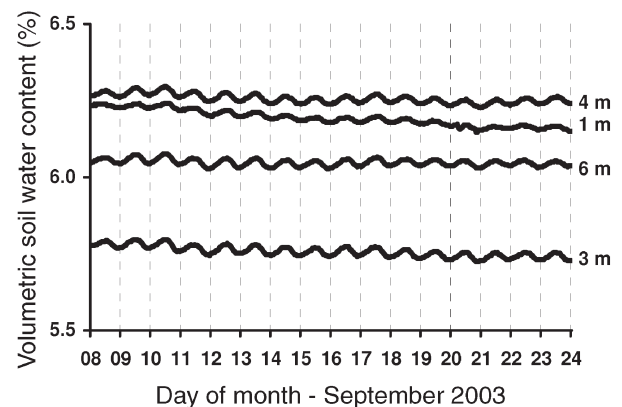


Figure 8. Daily fluctuations in volumetric soil water content observed at the end of summer 2003. Curves derived from sensors installed below the ground surface (0.35 m) at different distances from the trunk of one *Q. ilex* tree (tree crown projection radius is 4.2 m). Vertical dashed lines indicate midnight.

modeled the spatiotemporal groundwater balance in the Sardon catchment, near Salamanca, Spain, where tree vegetation consisted of *Q. ilex* and *Q. pyrenaica*.

The daily fluctuations in the topsoil water content (0.35-m depth) under *Q. ilex* during the summer drought (Figure 8) suggest that some of the groundwater lifted by the roots was released into the upper soil layers (as a result of a water potential gradient) before it was reabsorbed by shallow roots and transpired by trees (hydraulic lift). These dynamic soil water changes can only be ascribed to a single tree effect, because understory vegetation had been cut and was non-existent during measurements. Ideally, hydraulic lift is demonstrated by monitoring soil water potential (psychrometers) rather than SWC, because the latter may reflect not only the variations in soil water but also of internal root water (Emerman and Dawson 1996, Caldwell et al. 1998). Nevertheless, we believe that our SWC measurements reflected variations in soil matric potential (Ryel 2004). Daily fluctuations in Ψ_s or SWC due to hydraulic lift typically show a nighttime increase and a daytime decrease (e.g., Emerman and Dawson 1996, Caldwell et al. 1998, Ishikawa and Bledsoe 2000, Ryel 2004). The nighttime recharge of topsoil, which occurs via roots, results from transfer of water originating from deep and moist soil or groundwater to the dry soil surface, whereas the daytime depletion results from tree transpiration. Figure 8 shows that the observed daily SWC fluctuations in surface soil under *Q. ilex* lagged behind this typical pattern: SWC rose from about midnight to midday and decreased from about noon to midnight. The time lag behind the typical pattern was about 4 to 5 hours. Soil water potential fluctuations reported by Ludwig et al. (2003) showed a similar offset in some cases. We hypothesize that the lag was caused by the mobilization of water stored in plant tissues in the flow path from roots to the transpiring leaves. It is well documented that sap flow at breast height usually lags behind leaf transpiration (e.g., Loustau et al. 1996, David et al. 1997). Likewise, water stored in tree boles lags behind changes in transpiration (Pereira and Kozlowski 1978). For similar reasons, it should be expected that the responses of SWC to transpiration would also lag changes in sap flow. Therefore, soil water uptake driven by transpiration may start late in the morning and last for some time into the night. Topsoil water recharge occurred from about midnight to the middle of the day when there was no water uptake from soil by shallow roots.

The possibility of an artifact caused by an effect of temperature on the soil water sensors was discarded because soil temperature fluctuations were out of phase with SWC fluctuations. At a nearby experimental site, maximum and minimum soil surface temperatures occurred in summer at about 2000 and 1000 h, respectively (Kurz-Besson et al. 2006).

Hydraulic lift under *Q. ilex* (i.e., daily SWC fluctuations) occurred up to 6 m from the stem (Figure 8), extending beyond the crown limits (crown radius = 4.2 m), presumably reflecting the spread of lateral shallow roots (Moreno et al. 2005). Hydraulic lift in soil under *Q. suber* at a nearby site has also been demonstrated (Kurz-Besson et al. 2006).

During the summer drought, both species relied on ground-

water sources, either through direct uptake by deep roots or absorption of hydraulically lifted water by shallow roots, or both. In groundwater-dependent ecosystems, water table declines may increase plant water stress, leaf shedding and even tree mortality (Zencich et al. 2002, Cooper et al. 2003). In the Mediterranean evergreen oak savannahs, the main threat comes from the enhanced severity of summer drought caused by climate change. For instance, the severe drought of 1994 resulted in 80% foliage loss and up to 15% tree mortality in *Q. ilex* stands of eastern Spain (Peñuelas et al. 2000, Martínez-Vilalta et al. 2003) and the severe drought of 2005 in western Iberia led to a strong decline in tree gas exchange at our site (unpublished data). The increasing scarcity of water resources in the region has led to increased groundwater extraction for human use, which further aggravates the climatic effects on shallow groundwater tables. All these changes may have a negative impact on the sustainability of evergreen oak ecosystems, because these trees seem to rely frequently on subsoil water sources.

Drought resistance strategies of Q. ilex and Q. suber

During the summer drought, $\Psi_{l,pd}$ (Figure 3), g_c (Figure 6) and E (Figures 1 and 2) were higher in *Q. ilex* than in *Q. suber*. Mediavilla and Escudero (2003) also found higher summer $\Psi_{l,pd}$ in *Q. ilex* than in *Q. suber* in a study carried out near Salamanca, Spain. However, under pre-drought conditions, *Q. suber* had a higher g_c than *Q. ilex*, which is in accordance with the more mesophytic leaves of *Q. suber*, as well as higher specific leaf area (SLA) and higher photosynthetic capacity, as observed in previous work (Faria et al. 1998, Vaz 2005). The higher water status of *Q. ilex* trees during the summer drought can be explained only by the possession by this species of a deeper or more effective root system compared with that of *Q. suber*, because climate, soil water (Figure 7) and groundwater level (Figure 1) were similar in the two experimental plots. It is well known that different courses of seasonal plant water status usually reflect different rooting habits (e.g., Canadell et al. 1996). Compared with *Q. suber*, the higher transpiration rates of *Q. ilex* during the summer drought (Figures 1 and 2) were mainly a result of the higher $\Psi_{l,pd}$ in this species (Figure 3), which resulted in higher sap flow driving forces (Figure 4). These higher sap flow driving forces in *Q. ilex* during the summer resulted in higher E despite a lower k (Figure 5). No difference between species was found in δD_{xyl} , δD_{sw} or δD_{gw} in August 2002.

Minimum leaf water potential is usually considered a cavitation threshold (Cochard et al. 1996, Salleo et al. 2000, Sperry 2000, Lopez et al. 2005), corresponding to the need for stomatal closure to prevent Ψ_l from falling below the cavitation threshold (Jackson et al. 2000, Buckley and Mott 2002). The m/b ratio remained close to the theoretical value of 0.6 throughout the spring and summer in both species (Table 1). This means that both *Q. ilex* and *Q. suber* were efficiently regulating Ψ_l while the drought progressed, thereby preventing xylem embolism (Oren et al. 1999). The Ψ_l cavitation threshold is species-specific (Tyree and Sperry 1989), and is lower in drought-adapted species (Sperry 2000, Lemoine et al. 2001).

There is always a safety margin between the minimum values of Ψ_1 observed in the field and complete xylem embolism (Sperry 2000). In our study, minimum leaf water potentials observed in the field were -3.5 and -3.0 MPa for *Q. ilex* and *Q. suber*, respectively. The lower value of $\Psi_{1,md}$ in *Q. ilex* suggest that this species is less vulnerable to embolism than *Q. suber*. This feature is confirmed by the vulnerability curves to embolism presented by Tyree and Cochard (1996) for both oak species.

Whole-tree hydraulic conductance did not vary much over time in either species, but it was significantly lower in *Q. ilex* than in *Q. suber* (2.28×10^{-5} versus 3.15×10^{-5} kg m⁻² s⁻¹ MPa⁻¹). Lower k values are acknowledged to be a drought tolerance feature (Nardini and Tyree 1999, Lemoine et al. 2001, Martinez-Vilalta et al. 2002). In dry environments, the ability to tolerate drought is more important than the ability to transport water rapidly (Nardini and Tyree 1999, Lemoine et al. 2001) and there is usually a trade-off between hydraulic efficiency and resistance to xylem cavitation (Martinez-Vilalta et al. 2002). Therefore, species with lower k values will tend to be less vulnerable to xylem embolism. Additionally, a low k helps to limit sap flow from roots to leaves, thereby promoting more conservative water use (Lemoine et al. 2001). In *Q. ilex*, k was lower and seasonal water use more conservative than in *Q. suber*. The reduction in E from spring to the end of summer was only about 65% in *Q. ilex* compared with about 80% in *Q. suber*.

In summary, *Q. ilex* ssp. *rotundifolia* seems to have more effective drought avoidance and drought tolerance mechanisms than *Q. suber*. This is in accordance with the geographical distribution and leaf phenology of these species: *Q. ilex* occupies dryer inland areas and has a leaf lifespan of more than 18 months, whereas *Q. suber* has a shorter leaf longevity (about 12 months), dominates in the wetter western areas and can be considered as transitional between evergreen and deciduous oaks (Pereira et al. 1987). Therefore, it may be expected that *Q. suber* will suffer more than *Q. ilex* if drought severity in these Mediterranean ecosystems increases.

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