

Transpiration in *Quercus suber* trees under shallow water table conditions: the role of soil and groundwater

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Abstract:

Water is one of the major environmental factors limiting plant growth and survival in the Mediterranean region. *Quercus suber* L. woodlands occupy vast areas in the Iberian Peninsula, frequently under shallow water table conditions. The relative magnitude of soil and groundwater uptake to supply transpiration is not easy to evaluate under these circumstances. We recently developed a conceptual framework for the functioning of the root system in *Q. suber* that simulates well tree transpiration, based on two types of root behaviour: shallow connected and deep connected. Although this significantly improved knowledge on the functional traits of Mediterranean *Q. suber*, the approach has the limitation of requiring root sap flow data, which are seldom available. In this work, we present alternative methodologies to assess if trees are connected to groundwater and to estimate the soil and groundwater contributions to tree transpiration. We provide evidence on the tree unrestricted access to groundwater solely based on meteorological, stem sap flow and leaf water potential data. Using a soil mass balance approach, we estimated the yearly soil and groundwater contributions to tree transpiration: 69.7% and 30.3%, respectively. Groundwater uptake became dominant in the dry summer: 73.2% of tree transpiration. Results reproduce extremely well those derived from root modelling. Because of its simplicity both in formulation and data requirements, our approach is potentially liable to be adapted to other groundwater-dependent Mediterranean oak sites, where interactions between land use and water resources may be relevant. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS cork oak; sap flow radial profile; tree water use; water balance; tree water sources; ecohydrology

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INTRODUCTION

Water is one of the major environmental factors limiting plant growth and survival in Mediterranean climate regions (Mooney, 1983). Plants are subjected to a climatic seasonality and a recurrent asynchrony between water supply and demand. Mediterranean evergreen oaks developed several mechanisms to cope with seasonal summer drought, restraining water losses and/or maximizing water absorption through deep rooting (Walter, 1973; Infante *et al.*, 1997; David *et al.*, 2007; Limousin *et al.*, 2009). If the water table is within the reach of roots, these oaks may use groundwater to minimize summer water

deficit (Scott *et al.*, 2003; David *et al.*, 2004, 2007; Lubczynski and Gurwin, 2005; Miller *et al.*, 2010). Water uptake from this water reservoir may be relevant for the aquifer water balance and compete with other urban and agricultural water uses (Newman *et al.*, 2006; Lubczynski, 2009; García-Ruiz *et al.*, 2011).

Quercus suber L. (cork oak) woodlands occupy vast areas in the Iberian Peninsula and in western North Africa, the largest being located in Portugal (over 700×10^3 ha) (AFN, 2010). These ecosystems have a high socio-economic and conservation value, supporting high levels of biodiversity and acting as a source of income for rural populations (Bugalho *et al.*, 2011). A sparse stratum of *Q. suber* trees supporting the cork industry co-exists with an understory of grasses or shrubs. Although the potential distribution of the species includes almost the entire country (Natividade, 1950), *Q. suber* woodlands are mainly found along the lowlands of the

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Tagus and Sado river basins (AFN, 2010), frequently occupying areas with shallow water tables (WWF, 2010). Under these circumstances, ecosystem water use and sustainability are likely to be highly dependent on groundwater uptake by trees (Zencich *et al.*, 2002; Scott *et al.*, 2003; Lubczynski, 2009). The quantification of the relative magnitude of soil and groundwater uptake to supply seasonal transpiration is not an easy task. Stable isotopes are a valuable tool to identify and quantify the different sources of water use (soil or groundwater) (Zencich *et al.*, 2002; Kurz-Besson *et al.*, 2006; David *et al.*, 2007; Do *et al.*, 2008). However, the high cost of the analyses makes it difficult to obtain a continuous/integrated dataset. Recently, David *et al.* (2013) built up a conceptual framework for the functioning of the root system in *Q. suber* trees based on two types of root behaviour: shallow connected (linked to surface soil) and deep connected (linked through sinkers to groundwater). This modelling approach successfully estimated whole tree stem sap flow from root sap flow. Furthermore, the model allowed the continuous (daily) estimation of soil water and groundwater uptake as well as the magnitudes of hydraulic lift and hydraulic descent. Results showed that *Q. suber* trees used predominantly soil water during most of the year and groundwater in summer (performing hydraulic lift) when the surface soil was dry. Although these results represent a significant improvement on the knowledge of the functional traits of Mediterranean *Q. suber* woodlands, the used modelling approach has the limitation of requiring root sap flow, which is seldom available, as an input data. Therefore, it would be useful to develop alternative/simpler methodologies, using more commonly available data to (1) assess if tree roots are connected to groundwater and (2) estimate soil and groundwater contributions to the whole tree transpiration. In the present work, we will try to fulfil these two objectives using meteorological, soil water storage capacity, stem sap flow and leaf water potential data. Because these data and those reported in David *et al.* (2013) were collected at the same experimental site, results can be cross-checked for validation. The site is located over the Tagus aquifer – East of Lisbon. This aquifer is the largest groundwater reservoir in Portugal (9500 km² in area, from 6° 30' to 9° 40' W and 37° 00' to 40° 56' N (Simões, 2003)) being the main source of water supply for local domestic, industrial and agricultural uses (Ribeiro, 2009). Approximately 35% of its surface is occupied by *Q. suber* woodlands (WWF, 2010).

The experiment was conducted in mature *Q. suber* trees. Environmental (climate, soil moisture and groundwater) and ecophysiological (sap flow and leaf water potentials) measurements were carried out over a period of 18 months. We hypothesized that (1) the quantification of soil and groundwater uptake per tree could be possible

based on a simple soil mass balance approach requiring only meteorological, soil water retention capacity and stem sap flow data, and (2) even under well-watered conditions, stomata might still have a role in regulating tree water use.

MATERIAL AND METHODS

Experimental site

The experimental site is located at the largest *Q. suber* woodland near Lisbon, Central Portugal, in the estate of Companhia das Lezírias (38° 50' N; 8° 49' W, approx. 50 km E of Lisbon). Site topography is flat. The study area is a typical savannah-type ecosystem, with a sparse *Q. suber* canopy of 30 trees ha⁻¹ and tree crown cover of 29%. The understory is composed almost exclusively of grasses. The soil is a well-drained deep Haplic Arenosol (IUSS Working Group WRB, 2006) with a low water retention capacity. A shallow water table stands over a thick clay layer located at 9 m depth.

Climate is of Mediterranean type with wet, mild winters and dry, hot summers. Long-term (1951–1980, for the nearest meteorological station, Pegões) mean annual rainfall is 708 mm year⁻¹ (mainly concentrated in the period from October to April), open water evaporation is 1347 mm and air temperature is 15.6 °C (INMG, 1991). Monthly average temperatures range from 9.9 °C in January to 22.0 °C in August.

Plant material

Four mature *Q. suber* L. trees were intensively monitored from March 2007 to September 2008, encompassing two dry seasons. Seven additional trees were randomly selected to assess the representativeness of the water status of the intensively studied trees (through leaf water potential measurements). Average trunk diameter at breast height, crown-projected area and tree height of the four intensively studied trees were 0.73 ± 0.18 m, 208.1 ± 32.4 m² and 12.82 ± 1.16 m, respectively. Tree leaf area index, on a crown-projected area basis, was estimated by destructive sampling at the end of the experiment: 5.1 m² m⁻² (David *et al.*, 2012).

Meteorological measurements

Meteorological variables were continuously monitored at the site. An automatic weather station was set up at the top of a 16 m high scaffold tower to perform measurements on solar radiation (pyranometer CM6B, Kipp and Zonen, Delft, The Netherlands), net radiation (net radiometer Q7, REBS, Seattle, USA), wind speed (anemometer A100R, Vector Instruments, Rhyll, UK), and dry and wet bulb temperatures (aspired psychrometer

H301, Vector Instruments, Rhyl, UK). Rainfall (tipping-bucket rain gauge ARG100, Environmental Measurements, Gateshead, UK) was measured at ground level. Measurements were recorded as 10-min averages [temperature ($^{\circ}\text{C}$), solar radiation (R_s , W m^{-2}) and wind speed (m s^{-1})] or totals [rainfall (mm)] in a CR10X data logger (Campbell Scientific, Shepshed, UK). Air vapour pressure deficit (D , Pa) was calculated from dry and wet bulb temperatures.

Soil moisture

Water retention curves were determined in undisturbed soil samples, collected at 0.25, 0.50, 0.75 and 1.00 m depths, using Ceramic Plate Extractors (Soil Moisture Equipment Corp., Santa Barbara, USA) and applying extraction pressures of 5, 10, 33 and 1500 kPa (Table I). Bulk density, calculated after drying ($105 \pm 3^{\circ}\text{C}$) and weighting undisturbed soil samples collected at each depth, varied between 1.59 and 1.65 g cm^{-3} along the profile.

Volumetric soil water content was continuously assessed from late spring (June) 2007 onwards using soil moisture sensors [ECH₂O (EC-20), Decagon Devices, Inc., Pullman, USA]. Twelve probes were installed along three vertical profiles underneath tree canopy, at 0.25, 0.50, 0.75 and 1.00 m depths. Probes, measuring the dielectric constant (mV) of the soil, were connected to a CR23X data logger (Campbell Scientific, Shepshed, UK) to record 30-min averages. Volumetric soil water content ($\text{m}^3 \text{ m}^{-3}$) for each sensor was obtained using site-specific conversion equations established for each depth from water retention curves and periodic gravimetric determinations carried out from 0.1 to 1.1 m depth, every 0.2 m approximately once a month.

Volumetric soil moisture content was also measured periodically (usually weekly) in an open area, between the trees, through a PR1 Profile Probe (Delta-T Devices, Cambridge, UK) at the depths of 0.2, 0.4, 0.6 and 1.0 m in a thin-wall access tube. Measurements were also calibrated against gravimetric measurements.

Field soil moisture data are always prone to quantitative inaccuracies both due to instrumental errors and random

spatial variability (Gruber *et al.*, 2013). Therefore, these data were not used for quantitative purposes but only to characterize the approximate patterns of soil moisture variation in the different soil layers.

Groundwater table

Water table level variation was monitored in a 9 m deep borehole using a pressure transducer (PDCR 830, Campbell Scientific, Shepshed, UK). It measures the difference in pressure between the atmosphere and the depth of the sensor. Fluctuations of the water table level (m) were stored as 30-min averages in a CR10X data logger (Campbell Scientific, Shepshed, UK).

Sap flow

Tree stem sap flow was measured combining the thermal dissipation method (TD; Granier, 1985) to measure sap flow density in the outer xylem, with the heat field deformation method (HFD; Nadezhdina *et al.*, 1998) to assess the sap flow radial profile (sapwood conductive depth), enabling the conversion of sap flow density into sap flow.

Sap flow density was continuously measured from April 2007 till the end of September 2008 in four *Q. suber* trees. Two TD sensors (UP GmbH, Landshut, Germany) were radially inserted in the north-facing and south-facing stem sides of each tree, approx. 130 cm above soil surface. Sensors consisted of a pair of 20 mm long and 2 mm diameter probes, each one containing a copper-constantan thermocouple, inserted in the conducting xylem. The upper probe was heated to a constant power, whilst the lower one, 10 cm apart, remained at trunk and sap temperature. The temperature difference between each pair of probes was recorded as 30-min averages in CR10X and CR23X data loggers (Campbell Scientific, Shepshed, UK). Sap flow density in the outer 20 mm of conductive xylem was calculated based on the recorded averages of temperature difference and the maximum temperature difference between probes over 10-day periods (see Granier 1985, 1987, for full details).

The HFD method (Nadezhdina *et al.*, 1998) records changes in the heat field, caused by the moving sap, around a continuous linear heater inserted in tree stem. The deformation of the heat field is evaluated by two pairs of differential thermocouples, which measure the temperature difference in axial (symmetrical) and tangential (asymmetrical) directions (see Nadezhdina *et al.*, 1998, 2002, 2012, for further details). Based on these differences, sap flow per a certain stem section ($\text{g cm}^{-1} \text{ h}^{-1}$) and sap flow density ($\text{g cm}^{-2} \text{ h}^{-1}$) are derived.

Sap flow density radial profile was measured in the four *Q. suber* trees during March 2007. One multi-point HFD sensor, containing six equally spaced thermocouples (10 mm apart) (Dendronet, S.R.O., Brno, Czech Republic),

Table I. Volumetric soil water content ($\text{cm}^3 \text{ cm}^{-3}$) of soil for different depths and different soil suctions (-5 , -10 , -33 and -1500 kPa), at the Lezírias site

| Soil depth (m) | Soil water content ($\text{cm}^3 \text{ cm}^{-3}$) | | | |
|----------------|--|-----------|-----------|-------------|
| | -5 kPa | -10 kPa | -33 kPa | -1500 kPa |
| 0.25 | 0.055 | 0.046 | 0.033 | 0.009 |
| 0.50 | 0.054 | 0.037 | 0.020 | 0.006 |
| 0.75 | 0.063 | 0.046 | 0.025 | 0.006 |
| 1.00 | 0.074 | 0.058 | 0.034 | 0.008 |

was radially inserted in stem sapwood approx. 130 cm above soil surface. The same sensor was used to record sap flow density in 4/5 azimuths/tree (depending on stem diameter) for at least one clear sky day in each position. The first measuring point inside cambium varied from 3 to 5 mm. Data were stored at 5-min intervals in a Unilog Midi-12 data logger (EMS Co., Brno, Czech Republic).

The seasonal variation in the radial profile of sap flow density was monitored in one of the trees. Four multi-point HFD sensors (containing six equally spaced, 8 or 10 mm, thermocouples) were installed in tree stem xylem in the SE, SW, NE and NW azimuths in March 2007 and maintained until September 2008. Thirty-min temperature differences were stored in a CR10X data logger (Campbell Scientific, Shepshed, UK).

To estimate whole tree sap flow (F), the sap flow in the outer 20 mm of the xylem (TD method) was divided by the ratio between sap flow in this xylem layer and sap flow in the whole conductive area (estimated from the radial profiles obtained by HFD sensors). Average sap flow rates of the four sampled trees were calculated for 30-min intervals and integrated on a daily basis. Sap flow was expressed per unit of crown-projected area (mm day^{-1} or mm h^{-1}). Under steady state-conditions, stem sap flow (F) equals tree transpiration (T).

Leaf water potential

Seasonal variation of tree water status was assessed by measuring leaf water potential (Ψ_l , MPa) approximately on a monthly basis. Measurements were carried out in the selected trees (see Section on Plant Material) at predawn ($\Psi_{l, \text{pd}}$) and around midday ($\Psi_{l, \text{md}}$), using a Scholander pressure chamber (PMS 1000, PMS Instruments, Corvallis, OR, USA) (Scholander *et al.*, 1965). At each sampling time, three to four leaves per tree were collected and immediately measured. To avoid artificial variability caused by hydrostatic water potential, leaves were collected at similar heights aboveground from the south-facing side of the crown of each tree.

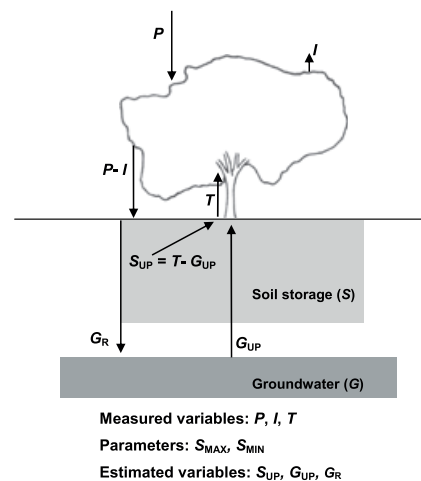
Predawn leaf water potential, $\Psi_{l, \text{pd}}$, is usually assumed to be in equilibrium with soil water potential (Ψ_s) and, hence, used as a surrogate for Ψ_s (Ritchie and Hinckley, 1975). However, this assumption may be invalid under conditions of night time transpiration (Donovan *et al.*, 2001). To test for equilibrium, we measured $\Psi_{l, \text{pd}}$ in two summer nights per year, in covered (aluminium foil) (Ψ_{xy1}) and uncovered ($\Psi_{l, \text{pd}}$) leaves. The difference between $\Psi_{l, \text{pd}}$ and Ψ_{xy1} for all sampling days was not significant. This suggests equilibrium in the whole plant–soil continuum, confirming that, in our case, $\Psi_{l, \text{pd}}$ is an adequate surrogate for Ψ_s . Additionally, during the whole study period, nocturnal transpiration was usually zero, probably because night time vapour pressure deficit was

consistently low (only one night with $D > 1000$ Pa during the study period).

Estimation of soil water and groundwater contributions to tree transpiration

Estimation of soil water (S_{UP}) and groundwater (G_{UP}) uptake by the average of sampled trees was performed according to the water balance scheme shown in Figure 1. The mass balance structure follows the simplified conclusions derived from the root functioning model of David *et al.* (2013): trees use preferentially soil water and groundwater only when the soil storage is depleted. Input data were rainfall (P), interception loss (I), tree transpiration (T) and soil water storage capacity ($S_{\text{MAX}} - S_{\text{MIN}}$). P and T were measured, being T the average of the four sampled trees. Interception loss (I) was estimated as 26.3% of P , based on measurements in *Q. ilex* trees (Pereira *et al.*, 2009), which are similar to *Q. suber*.

Soil water storage capacity was calculated from the depth of soil profile and moisture retention data at different suctions (Table I). Because soil moisture under the trees seems to respond to transpiration demand up to 1 m depth (Figure 2), soil water storage capacity was calculated for this soil depth. The horizontal extent (projected area) of the soil compartment was considered equal to that of the canopy, because most of the



Daily water balance calculations:

- Initial daily soil water storage S_0 = final storage of previous day S_f (-1)
- First S update: $S_1 = S_0 + (P - I) - T$
- IF $S_1 > S_{\text{MAX}}$, $G_R = S_1 - S_{\text{MAX}}$; Else $G_R = 0$
- IF $S_1 < S_{\text{MIN}}$, $G_{\text{UP}} = S_{\text{MIN}} - S_1$; Else $G_{\text{UP}} = 0$
- $S_{\text{UP}} = T - G_{\text{UP}}$
- Final daily soil storage $S_f = S_1 - G_R + G_{\text{UP}}$

Figure 1. Schematic representation of the water balance framework used for the calculation of soil water uptake (S_{UP}), groundwater uptake (G_{UP}) and groundwater recharge (G_R). Used input variables were rainfall (P), interception loss (I) and tree transpiration (T). Soil water storage parameters are S_{MAX} and S_{MIN}

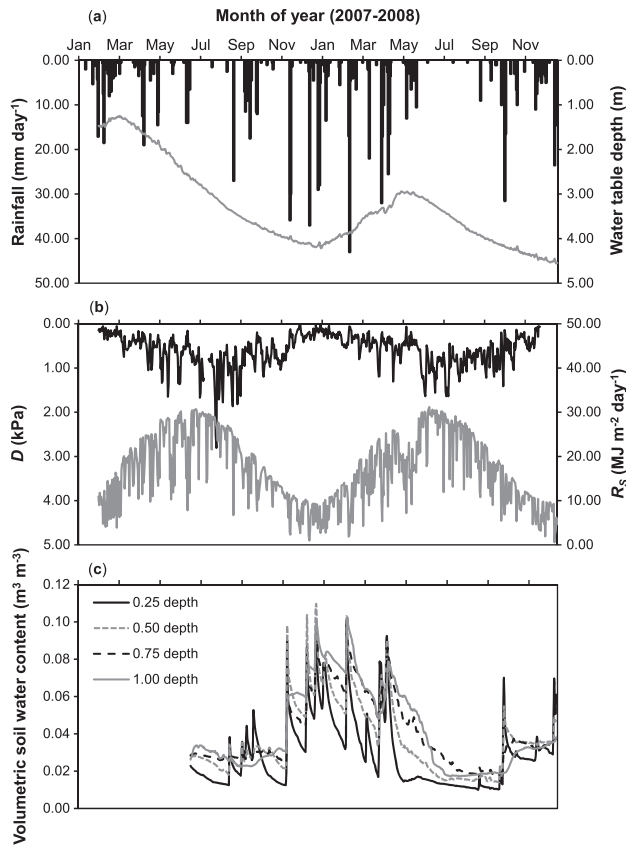


Figure 2. Seasonal variation of daily (a) rainfall (columns) and water table depth (line); (b) vapour pressure deficit (D) (black line) and solar radiation (R_s) (grey line); and (c) average volumetric soil water content at four different depths

superficial roots bend 90° down near the crown limits, turning into sinkers (see David *et al.*, 2013). The maximum soil storage was considered equal to field capacity and the minimum to the wilting point. However, there is some controversy on what is field capacity and on how it should be evaluated (Hillel, 1982). Traditionally, it has been considered equal to the moisture retention at -33 kPa suction, but moisture contents at -10 or -20 kPa suctions have been considered by some authors as the more appropriate for sandy soils (see Zekri and Parsons, 1999). Because the controversy remains, we optimized the values of field capacity to use in our water balance as those that provided the best fit of the soil and groundwater uptake estimates (S_{UP} and G_{UP}) from this water balance approach with those from the root modelling of David *et al.* (2013). We tested the water balance for the -10 , -20 (interpolation between -10 and -33) and -33 kPa moisture curves (Table I). The best results were obtained for the conventional moisture retention at -33 kPa suction. Soil water storages (S), at field capacity and wilting point, in the whole profile (mm) were calculated from soil moisture (Θ_i), at -33 and -1500 kPa suctions, respectively (Table I),

and depth (z_i , mm) of each sampled soil layer (i) as $\sum \Theta_i z_i$. To simplify the calculations, S_{MIN} for the considered soil water compartment was set to zero ($S_{MIN} = 0$) and S_{MAX} to $S_{FieldCapacity} - S_{WiltingPoint}$ ($S_{MAX} = 21$ mm). Some additional assumptions/simplifications on the water balance of Figure 1 are as follows:

- (a) surface runoff is not considered because of the flat topography of the area and the high infiltration capacity of arenosols (on average 137 mm h^{-1} ; FAO, 2001);
- (b) lateral soil water movements were not accounted for because differences in soil moisture content between soil under tree canopy and in the open were always less than $\pm 0.03 \text{ m}^3 \text{ m}^{-3}$ (at all depths), both in the wet and dry season, which are within the expectable experimental errors in soil moisture (0.02 – $0.06 \text{ m}^3 \text{ m}^{-3}$, Gruber *et al.*, 2013) (see Section on Soil Moisture); and
- (c) understory evaporation is neglected because leaf area index (LAI) of the studied trees is high (5, on a crown-projected area basis), and crown width is large compared to tree height; therefore, very little radiation and evaporation should be expected at ground level beneath the crowns. In a recent review, Baldocchi and Ryu (2011) reported that evaporation from understory decreases with increasing LAI . Small understory annual evaporation values are reported for a Mediterranean oak savannah (less than 20% of total evaporation, LAI of 0.7), a deciduous forest in Tennessee (10% of total evaporation, LAI of 6) and a boreal pine forest in Sweden (10–15% of total evaporation, LAI not reported).

Calculated values were soil water uptake (S_{UP}), groundwater uptake (G_{UP}) and groundwater recharge (G_R). Calculations were carried out daily with all variables in millimetres per unit of crown-projected area. Daily running water balance calculations were performed as follows (Figure 1):

- Initial daily soil water storage S_0 = final storage of previous day $S_F(-1)$
- First S update: $S_1 = S_0 + (P - I) - T$
- IF $S_1 > S_{MAX}$, $G_R = S_1 - S_{MAX}$, Else $G_R = 0$
- IF $S_1 < S_{MIN}$, $G_{UP} = S_{MIN} - S_1$, Else $G_{UP} = 0$
- $S_{UP} = T - G_{UP}$
- Final daily soil storage $S_F = S_1 - G_R + G_{UP}$

Daily calculated values were integrated monthly, seasonally and yearly. G_{UP} , S_{UP} and G_R estimates will only be accurate if all the used data and parameters (measured/estimated) as well as the underlying assumptions are correct. To check for validity, our results were compared with those modelled from root functioning (David *et al.*, 2013).

Canopy conductance

Given the high degree of coupling between the atmosphere and the canopy of savannah-type woodlands (Infante *et al.*, 1997), transpiration (T , mm h^{-1}) can be approximated by (McNaughton and Jarvis, 1983; Jarvis and McNaughton, 1986):

$$T = g_c D \frac{\rho c_p}{\lambda \gamma} \quad (1)$$

where g_c is the canopy conductance (m s^{-1} , expressed per unit of crown-projected area), D is the vapour pressure deficit of the air (Pa), ρ is the density of air (kg m^{-3}), c_p is the heat capacity of water in air ($\text{J kg}^{-1} \text{ }^\circ\text{C}^{-1}$), λ is the latent heat of evaporation of water (J kg^{-1}) and γ is the psychrometric constant ($\text{Pa }^\circ\text{C}^{-1}$). Based on Equation 1, and considering that at midday $T=F$, we estimated midday canopy conductance ($g_{c,m}$) from June 2007 to September 2008, discarding days with rainfall or D lower than 500 Pa.

Stomata usually respond to increases of the vapour pressure deficit between leaf and air by partial closure. The sensitivity of the response (i.e. the magnitude of the decrease) of $g_{c,m}$ to increasing D (kPa) was determined by fitting the following equation to the existing data (Oren *et al.*, 1999):

$$g_{c,m} = b - m \ln D \quad (2)$$

where the slope of the line is $dg_{c,m}/d \ln D = -m$ and b is the intercept. The parameter m quantifies the sensitivity of $g_{c,m}$ to D , and b is a reference conductance ($b = g_{c,ref}$) at $D = 1$ kPa. Although stomatal sensitivity varies considerably both within and between species, Oren *et al.* (1999) have shown that the m/b ratio is close to 0.60, for a wide range of mesic species, when stomata are regulating leaf water potential above the cavitation threshold.

RESULTS

Environmental data

Environmental variables (Figure 2) followed a marked seasonal pattern, typical for a Mediterranean-type climate region, with rainfall mainly concentrated in autumn–winter and evaporative demand (D and R_s) peaking during late spring–early summer (Figure 2a, b). Annual rainfall was 441.5 mm in 2007 and 576.0 mm in 2008, representing 62% and 81%, respectively, of the long-term average. Although the spring was wetter in 2008 (174.0 mm) than in 2007 (121.0 mm), the summer period was particularly dry and prolonged in 2008, with only 17.5 mm of rain from 1 June to 30 September (contrasting with 145.0 mm during the same period in 2007). The water table depth was at its highest (1.3 m) in early 2007, declining afterwards until next winter (4.2 m). Groundwater level rose

in spring 2008, although with a delayed response to wet season rainfall, reaching a lower peak (3.2 m) than in the previous year. The lowest value (around 4.5 m) was observed after the summer/autumn period of 2008. Soil water content reflected rainfall seasonality, recharging the whole profile (till 1 m depth) during the wetter periods and reaching minimum values during the dry months (Figure 2c). During the dry season, the deep soil layers (0.75 and 1.00 m) showed slightly higher water contents than the surface ones (0.25 and 0.50 m).

Tree transpiration

The radial profiles of sap flow density (HFD method) observed in March 2007 in the four *Q. suber* trees and in the different azimuths showed that the water transport occurred mainly in the outer xylem layers, peaking around 10–16 mm below the vascular cambium and declining gradually into the heartwood (data not shown). From the radial profiles, the average sapwood depth was estimated to be 6.5 cm (varying from 5.7 to 6.9 cm among individual trees).

The seasonal variation of the average radial profile of sap flow was monitored in one of sampled trees and showed a shift from the pattern observed in March (Figure 3, grey line) as time progressed. After the initial 3 months (June 2007), the flow in the two outer xylem layers shifted upwards, being higher near the vascular cambium and declining towards the heartwood (Figure 3, black line). This pattern remained stable, on hourly, daily and seasonal basis, from June 2007 onwards. Because of the uncertainty on the causes of the observed shift in the sap flow radial profile, data on the TD sap flow are only presented from June 2007 onwards, that is, when the HFD radial profile became stable. We assumed that a similar shift also occurred in the other three trees in the outer two measuring points. Upon this correction, the ratio of sap

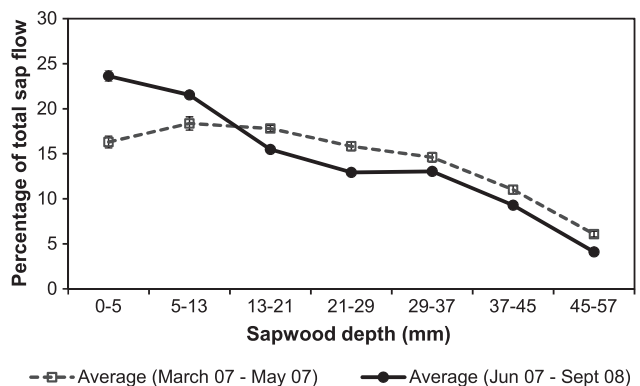


Figure 3. Seasonal variation of the radial sap flow profile (heat field deformation method, percentage of total sap flow) in one of the sampled trees: average between March (sensor installation) and May 2007 (dashed grey line, open squares) and between June 2007 and September 2008 (black line, solid circles). Error bars are standard errors

flow in the outer (0–20 mm) xylem layers and the total sap flow (in the whole conductive area) varied between 0.51 and 0.61 in the four sampled trees.

Tree sap flow data obtained by the two sap flow methods, that is, the thermal dissipation method scaled up to the whole conductive area (average of four trees) and the heat field deformation method (one tree), showed synchronized patterns throughout the experimental period (Figure 4a). A close relationship (slope = 1.11; $R^2 = 0.71$) (Figure 4b) was observed between daily sap flow estimated by the two methods for the same tree, with the TD method estimates slightly lower (on average 11%) than those by HFD, being this difference bigger for the higher values.

Daily sap flow peaked in late spring–early summer (June to July) of both years, following closely the seasonal patterns of solar radiation and vapour pressure deficit (Figures 2b and 4a). Average daily summer transpiration (June to September) did not differ between years [0.85 and 0.84 mm day⁻¹ (TD) and 0.86 and 0.82 mm day⁻¹ (HFD) in 2007 and 2008, respectively], in spite of the lower rainfall and soil moisture content in summer 2008 (Figure 2). Maximum transpiration rates (July) were around 1.1 and 1.3 mm day⁻¹ in 2007 and

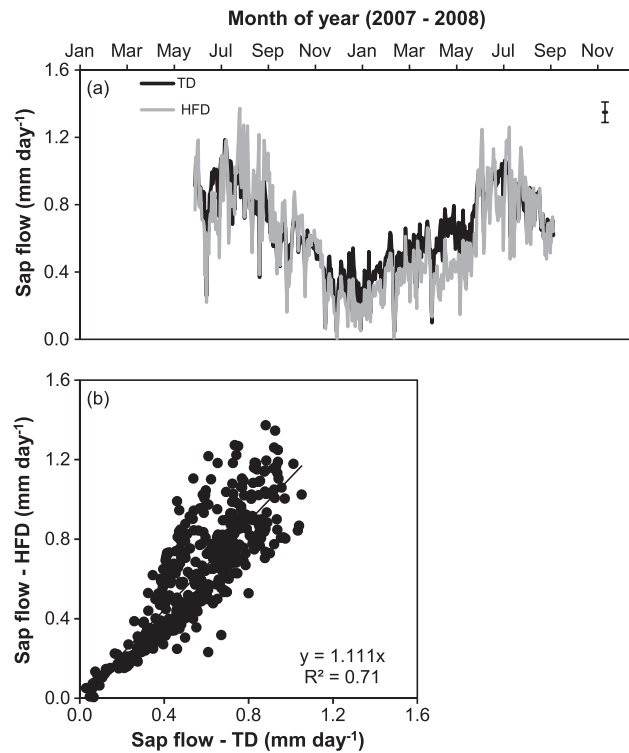


Figure 4. Tree transpiration (sap flow) of *Quercus suber* trees: (a) seasonal variation of daily values using the thermal dissipation (TD – average of four trees, black line) and the heat field deformation (HFD – one tree, grey line) methods (June 2007 to September 2008). Error bar is the average standard error for TD data (four trees); (b) relationship between daily values estimated by the two sap flow methods for the same tree. Sap flow is expressed per unit of crown-projected area

2008, respectively. Daily sap flow was linearly related with daily solar radiation ($R^2 = 0.86$) (Figure 5a). The relationship between daily sap flow and D was asymptotic, with sap flow positively responding to increases in D up to 1000 Pa. When D approached 1500 Pa, the response ceased almost completely (Figure 5b).

Leaf water potential

Predawn leaf water potential ($\Psi_{1, \text{pd}}$) remained high and approximately constant (around -0.2 MPa) throughout most of the experimental period (Figure 6). Minimum values of $\Psi_{1, \text{pd}}$ were observed after the dry seasons and were above -0.5 MPa in both years. This pattern of variation was also observed in the seven surrounding trees (slope = 1.08 and $R^2 = 0.94$, in a linear regression through the origin). These results showed that $\Psi_{1, \text{pd}}$ in the four intensively studied trees is representative of the water status of the surrounding trees. Seasonal variation in midday leaf water potential ($\Psi_{1, \text{md}}$) reflected differences in the atmospheric conditions, tree water use and stomatal regulation. During most of the study, $\Psi_{1, \text{md}}$ values ranged between -2.0 and -3.0 MPa (Figure 6), reaching a minimum value, -2.98 MPa, in June 2008.

Soil water and groundwater contributions to tree transpiration

Figure 7 shows the estimated monthly values of the water balance components for the average of sampled

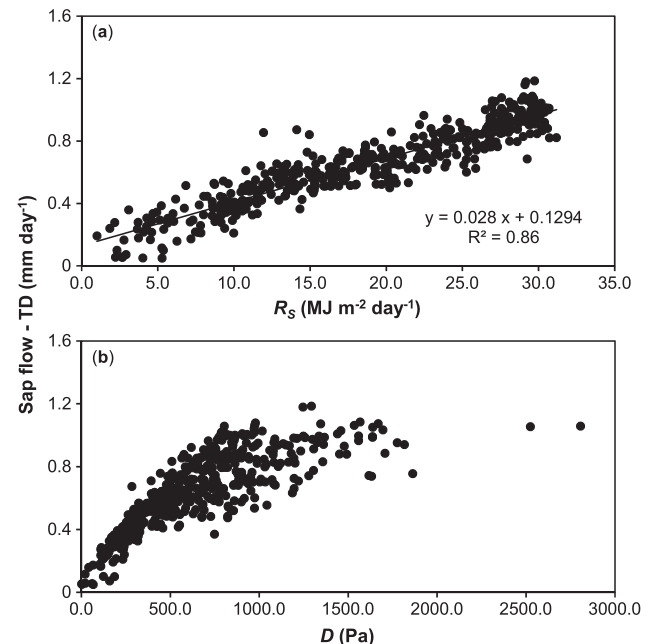


Figure 5. Relationships between tree daily sap flow [thermal dissipation (TD) method, June 2007 to September 2008] and (a) solar radiation (R_s) and (b) average vapour pressure deficit (D). Sap flow is expressed per unit of crown-projected area

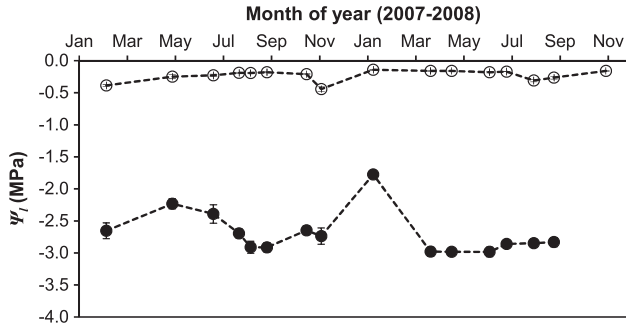


Figure 6. Seasonal variation of predawn ($\Psi_{l,pd}$, open symbols) and midday ($\Psi_{l,md}$, closed symbols) leaf water potential in *Quercus suber* during 2007 and 2008. Error bars are standard errors. Error bars in $\Psi_{l,pd}$ are contained within the size of symbols

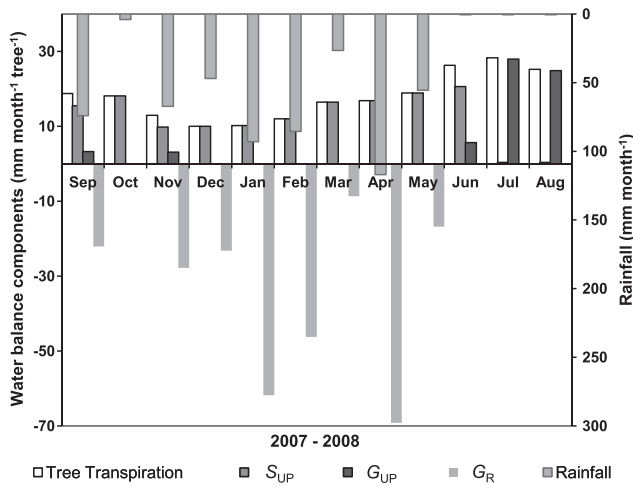


Figure 7. Monthly values (September 2007 to August 2008) of rainfall, average tree transpiration, groundwater uptake (G_{UP}), soil water uptake (S_{UP}) and groundwater recharge (G_R) according to water balance calculations following the scheme of Figure 1. Values are in mm month^{-1} , on a crown-projected area basis

trees (September 2007 to August 2008): rainfall (P), tree transpiration (T), soil water uptake (S_{UP}), groundwater (G_{UP}) and groundwater recharge (G_R).

Total yearly and summer values are shown in Table II.

Table II. Yearly and summer values for soil water uptake (S_{UP}), groundwater uptake (G_{UP}) and groundwater recharge (G_R), for the average of sampled trees, according to the scheme of Figure 1 (see Figure 7 for monthly values)

| Rainfall (P) | Transpiration (T) | Groundwater uptake (G_{UP}) | Soil water uptake (S_{UP}) | Groundwater Recharge (G_R) |
|---|-----------------------|---------------------------------|--------------------------------|--------------------------------|
| (a) Yearly values (September 2007 to August 2008) | | | | |
| 571.3 | 214.2 | 64.8 (30.3) | 149.4 (69.7) | 275.7 |
| (b) Summer values (June to August 2008) | | | | |
| 1.5 | 79.9 | 58.5 (73.2) | 21.4 (26.8) | 0.0 |

Measured rainfall (P) and average tree transpiration (T) are also given. Values are in millimetres per unit of crown area. Between brackets are per cent (%) of T .

Canopy conductance

As expected, midday canopy conductance decreased exponentially as vapour pressure deficit (D) increased. A unique relationship between daily $g_{c,m}$ (mm s^{-1}) and midday D (Pa) values was observed for *Q. suber* trees throughout the experimental period, irrespective of season (Figure 8). The absence of rainfall during the summer periods did not cause any further reductions in stomatal conductance, as stomatal response to D followed a unique trend during wet and dry seasons. The sensitivity of the response of $g_{c,m}$ to D (m , Equation 2) and the reference g_c at $D = 1 \text{ kPa}$ (b , Equation 2) were 1.47 and 2.53, respectively. The ratio m/b was 0.58, close to the reference value of 0.6.

DISCUSSION

Sap flow: methodological aspects

As stated in the introduction, the analyses performed in this work greatly depend on the accuracy of the measurements. This is particularly relevant in the tree transpiration estimates through sap flow measuring techniques, namely in what concerns the measurement of the sap flow radial profiles. The sap flow radial profile (Figure 3) showed a pronounced shift in the outer xylem in the initial 3 months after sensor installation, from March till June 2007. The observed shift may be due to (1) initially inefficient sensor insulation following cork removal for sensor installation, (2) new tissue formation around the sensor or a change on sensor position relative to cambium due to the spring growth, (3) a response to phenological activity (Dragoni *et al.*, 2009) or (4) the occurrence of non-typical patterns of soil moisture from March to May 2007, with outer xylem layers connected to shallow dry soil and inner xylem layers to wet deep soil (Nadezhdina *et al.*, 2007, 2008). The available information does not provide a sound explanation for the observed shift in sap flow radial profile. Because of these uncertainties, TD sap flow density data were only up

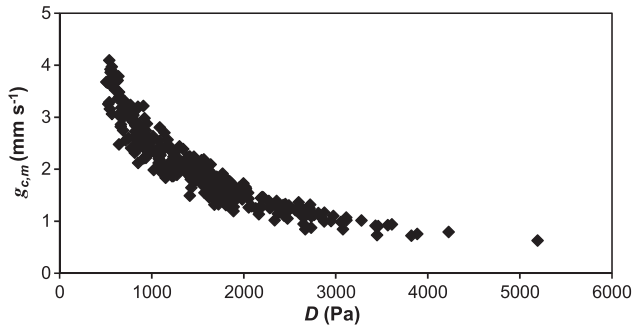


Figure 8. Relationship between daily midday canopy conductance ($g_{c,m}$) and midday vapour pressure deficit (D) for *Quercus suber*, from June 2007 to September 2008

scaled to sap flow when the HFD radial profile stabilized (hourly and daily), that is, from June 2007 onwards (Figure 3, black line). After June 2007, the variation of sap flow across the sapwood depth exhibited a typical and stable pattern with higher rates in the outermost xylem layers and a gradual decrease towards the heartwood (Figure 3), as has also been reported for *Quercus petraea* and *Q. robur* (Granier *et al.*, 1994), *Q. calliprinos* and *Q. ithaburensis* (Cohen *et al.*, 2008), and *Pinus pinaster* (Delzon *et al.*, 2004).

Daily sap flow density data showed some circumferential variations in all the studied trees. Although omitting the within-tree circumferential variations in stand sap flow estimates is reported to be a minor source of error, compared with radial and tree-to-tree sap flux variation (Kume *et al.*, 2012), we tried to minimize it by sampling at least two azimuths in all trees.

Sap flow estimates by the TD and HFD methods (Figure 4a) showed good agreement ($R^2 = 0.71$) (Figure 4b). In spite of recent reports on the possible underestimation of sap flow by the two methods (Steppe *et al.*, 2010; Vandegehuchte and Steppe, 2012), more precise sap flow measuring techniques are not yet available. The eddy covariance method could not be used at the site because of fetch requirements. Moreover, it would not discriminate the specific water use by the trees, which was our goal.

Tree access to groundwater

The single linear relationship between transpiration and solar radiation, the existence of a unique asymptote in the relationship between transpiration and vapour pressure deficit, the constancy of high transpiration irrespective of rainfall in summer and the maintenance of high $\Psi_{1,pd}$ values throughout the experimental period (Figures 2, 4, 5 and 6) provide evidence on the existence of unrestricted sources of water supply to tree roots (groundwater) in addition to soil water at the Lezirias site. We believe that the observation of these simple features may be used in many tree groundwater-dependent ecosystems around the

world to verify if there is or not an unrestricted tree groundwater uptake by trees during seasonal or occasional drought. Under drought, soil water storage coupled to rainfall will not be enough to sustain *per se* high tree water status and transpiration, and signs of water stress are liable to occur. Seasonal or occasional water stress in plants induce stomatal closure that reflects in a decrease in the slope of the relationship between transpiration and radiation (Zur *et al.*, 1983; Berbigier *et al.*, 1991; Horna *et al.*, 2011), a decrease in the slope and in the plateau of the relationship between transpiration and D (Infante *et al.*, 1997; Vose *et al.*, 2000; Horna *et al.*, 2011), and a decrease in predawn leaf water potentials (e.g. Infante *et al.*, 1997; Martínez-Vilalta *et al.*, 2003; Limousin *et al.*, 2009). If none of this occurs during the drought period (as in our case), it is because trees are freely accessing groundwater. At our site, the correctness of this inference was confirmed by sap flow measurements in roots and stable isotope data (David *et al.*, 2013). Ecosystems in which trees are groundwater dependent during seasonal or occasional drought have been found to occur in many parts of the world, in Mediterranean (e.g. Scott *et al.*, 2003; David *et al.*, 2004, 2007; Benyon *et al.*, 2006; Miller *et al.*, 2010) and semi-arid regions (e.g. Lubczynski, 2009) and in temperate forests (e.g. Dolman, 1988). However, tree roots may have access to groundwater and still show signs of water stress (if the access is somehow restricted) (e.g. David *et al.*, 2007). In those cases, the proposed method will not hold. The method holds only when groundwater access is unrestricted (e.g. David *et al.*, 2004, and this paper; see also Paço *et al.*, 2009, for a comparison of results of David *et al.*, 2004 and David *et al.*, 2007). Paço *et al.* (2009) further showed that the issue is not only the depth of the water table but also the existence of restrictions in root access to it, which depends also on the species (rooting depth, see Canadell *et al.*, 1996) and the nature (hardness) of the underlying rock/aquifer.

Soil water and groundwater contributions to tree and ecosystem transpiration

According to the mass balance formulation of Figure 1, we estimated the monthly contributions of the soil (S_{UP}) and groundwater (G_{UP}) pools of water to tree transpiration (T) from September 2007 to August 2008 (Figure 7). Following the underlying conceptual framework, groundwater uptake only took place in summer when the soil was dry. Estimated S_{UP} and G_{UP} amounted to 69.7% and 30.3% and to 26.8% and 73.2% of tree transpiration on an annual and summer basis, respectively. These estimates are consistent with those modelled from root functioning for the same site and for the same periods by David *et al.* (2013): monthly water balance (WB) estimates fitted well

against those from the root modelling (Roots) ($S_{UP(WB)} = 1.00 \times S_{UP(Roots)}$, $R^2 = 0.79$, $n = 12$; $G_{UP(WB)} = 1.05 \times G_{UP(Roots)}$, $R^2 = 0.92$, $n = 12$); yearly soil and groundwater contributions to T estimated by the two approaches were similar (69.7% and 30.3% by the water balance and 68.6% and 31.4% by root modelling, respectively). In summer, the groundwater contribution is slightly overestimated by the water balance approach compared with root modelling 73.2% and 64.6% of T , respectively (a per cent difference of 13.4%). The model reported in David *et al.* (2013) calculates the amount of hydraulic lift, but the mass balance formulation does not. Hydraulic lift was subtracted from soil water contribution and added to groundwater contribution in the root modelling results for the aforementioned comparisons. It also calculates the amount of hydraulic descent. In this respect, the two approaches may be seen as complementary. For instance, on a yearly basis (September 2007 to August 2008), our approach estimated the amount of total groundwater recharge (275.7 mm, Table II), whereas David *et al.* (2013) estimated the total annual hydraulic descent (83.2 mm), that is, about 30.2% of G_R . Our approach has the advantage of requiring much more commonly available data (rainfall, soil moisture retention parameters and tree transpiration), whereas the approach of David *et al.* (2013) needs the uncommonly available sap flow measurements in roots.

The good fitting between results from the simple mass balance approach of Figure 1 with those from root modelling (validation) means that the underlying assumptions/simplifications for the water balance are acceptable at the site level and that its structure captures the predominant functional features of the system. A continuous dialog exists between different emphases in ecological modelling: complexity *versus* simplicity, large scale (models of everywhere) *versus* site-specific models, and process understanding *versus* prediction and amount and quality of data requirements (Beven, 2007; Wainwright and Mulligan, 2013). These approaches are complementary and not mutually exclusive. In recent years, the most common modelling approach in environmental modelling was to try to incorporate all understanding on the complexity of systems with a multitude of variables and parameters that cannot be easily identified for a particular place (Beven, 2007; Wainwright and Mulligan, 2013). This may be useful when the objective is to try to capture most of the understanding about a particular system (usually highly instrumented) but is hardly useful for prediction (i.e. extrapolation of results both in time and in space) in other poorly instrumented sites. For prediction purposes, simple models that capture the dominant modes of a system and require frequently available data are extremely useful and relevant (Wainwright and Mulligan, 2013). The basic idea is to understand first, to be able to

simplify/apply/generalize later. In this work, we tried to follow these stepwise stages upon the understanding on system functioning gained from the previous root modelling of David *et al.* (2013). Within this line of reasoning, we believe that the simplicity of the conceptual framework of the mass balance of Figure 1, and its limited data/parameter requirements, may be advantageous for applications/predictions in other similar sites. As reported in the previous section, in a large number of ecosystems around the world, trees are groundwater dependent. At this stage, the presented water balance model is site specific, because it is based on specific assumptions and simplifications for our site. However, we think that (because of its simplicity) it can be easily adapted to other places, which will always have, nevertheless, some unique features as acknowledged by Beven (2007). For instance, a surface infiltration restriction can be easily added to predict surface runoff, if relevant; the spreading of lateral roots beyond the crown limits can be dealt through the water storage capacity of the soil compartment (considering depth and lateral extension and doing the calculations in units of volume instead of mm); and pasture evaporation can also be included (if known) particularly if the considered soil area has open areas exposed to radiation.

Interestingly, our mass balance approach recaps some similar/simple concepts put forward by Dolman (1988) in an earlier paper trying to explain transpiration during drought in a temperate oak forest in the Netherlands. We think that one of the key features on future applications will be the appropriate estimation of the maximum water storage capacity of the soil compartment used by roots (S_{MAX}). Outputs from the mass balance are quite sensitive to it. Problems may arise in the estimation of the depth and extension of the superficial root system and from the yet poorly understood concept and evaluation of field capacity. Hillel (1982) suggested that, in many cases, it will be up to the user to select the soil moisture storage that best suits his purposes, within acceptable limits. S_{MAX} was the only parameter somehow optimized in our approach although framed within the possible soil water contents at the suctions most commonly used. Best fits were obtained when S_{MAX} was calculated considering the classical volumetric water content at -33 kPa. Our results highlight that there are two distinct processes involved in groundwater recharge, at quite different response rhythms: the quick hydraulic descent, through roots, which amounts annually to about 30% of G_R , and the slower infiltration process down the soil profile (about 70% of G_R). Water infiltration into the soil takes about 2–5 days to reach the bottom soil layer (depending on initial soil moisture), as also reported by Zekri and Parsons (1999) (about 4 days for a 1.5 m deep sandy soil). The soil moisture profiles (field) did not seem adequate for the daily water balance closure calculations: they do

not capture the hydraulic descent, some transient water may come from previous rainfall days and measurements are prone to inaccuracies. In spite of its simplicity, the simple soil box formulation of Figure 1 seemed to work very well both in our study and that of Dolman (1988). However, further research is clearly needed on this key issue.

The mass balance approach presented in this work is not, and does not intend to be, the solution for the evaluation of the water use by trees in groundwater-dependent ecosystem (rarely or poorly addressed in current ecohydrological models). It should be rather viewed as a contribution, we believe innovative, to the modelling learning process referred by Beven (2007) on the behaviour of such ecosystems – interaction between sites and broader scales, interaction between complexity and simplicity, and data requirements. Only future research (application/adaptation/validation) will show how useful this approach will be for wider applications.

By focusing on the area we were working in, over the Tagus aquifer, a big diversity of vegetation types occurs, but 35% of its surface is *Q. suber* woodlands (WWF, 2010). Within the latter, it is not yet known the relative proportion of areas where trees are or not groundwater dependent. In future studies, this gap could probably be tackled by scanning leaf/crown temperatures in summer through large scale thermal imaging (Jones *et al.*, 2009; Costa *et al.*, 2013). Within this study, we did not intend to evaluate the overall impact of all vegetation types on the aquifer balance, but rather focus on the less understood ecosystems, where tree roots have direct access to groundwater. For these ecosystems, results show that trees use soil water during most of the year and groundwater in summer to cope with the seasonal drought. However, the use of groundwater will depend on the amount and distribution of summer rainfall. Because the severity of seasonal summer drought is predicted to increase in the Mediterranean, due to climate change (IPCC, 2007), the proportion of groundwater uptake by trees will also tend to increase. All presented data on tree water balance are expressed in millimetres per unit of crown area, but they can be easily transformed in millimetres per unit of ground area multiplying by the crown cover fraction (0.29, see Section on Plant Material). However, these data do not represent the whole ecosystem water balance because a significant part (71%) is occupied by pasture, which was not studied. This is particularly relevant for the annual water balance. However, during summer, grasses stop transpiring, and the tree component and ecosystem water balances will be the same (Paço *et al.*, 2009). Our results may be important both for ecosystem sustainability and for human activities also dependent on groundwater use (urban supply and irrigation) (Naumburg *et al.*, 2005; Lubczynski, 2009). Under this perspective, conflicts may arise between the

maintenance of groundwater-dependent ecosystems and anthropogenic water demanding activities (Hatton *et al.*, 1998; Le Maitre *et al.*, 1999; Martínez-Santos *et al.*, 2008; Hasselquist and Allen, 2009).

By quantifying the relationships between *Q. suber* woodlands and the underlying aquifer, our results may somehow contribute to more integrative planning approaches, considering both land use and water resources, in parts of the Tagus river basin.

Control of water losses

Even under non-limited water supply conditions, stomata may still need to regulate transpiration losses. There is an upper hydraulic limit to tree transpiration imposed by minimum leaf water potential and tree hydraulic conductance (Cruziat *et al.*, 2002). Stomata seem to act as pressure regulators preventing leaf water potential to fall below a cavitation threshold (Jackson *et al.*, 2000; Buckley and Mott, 2002). They do so by preventing imbalances at the leaf level between evaporative demand and maximum hydraulic pumping capacity (Buckley and Mott, 2002). The minimum leaf water potential observed in field conditions (−2.98 MPa at Lezirias) is usually considered a measure of its cavitation threshold (Salleo *et al.*, 2000; Sperry, 2000). Our results suggest that, even in the absence of water constraints, trees at Lezirias were regulating minimum leaf water potential near this constant minimum value (Figure 6).

An exponential decrease of stomatal conductance with D was observed at the Lezirias site, where canopy conductance was reduced to a unique closure plateau above $D = 1.5$ kPa (Figure 8), imposing a maximum transpiration rate above this D value (Figure 5b). During the dry season of both years at Lezirias, the m/b ratio was close to the reference value (0.6), which means that stomata were efficiently responding to D (Figure 8), regulating minimum Ψ_1 above its cavitation threshold (see Oren *et al.*, 1999).

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