



## Hydraulic lift in cork oak trees in a savannah-type Mediterranean ecosystem and its contribution to the local water balance

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### Abstract

The aim of this study was to identify the sources and depth of water uptake by 15-years old *Quercus suber* L. trees in southern Portugal under a Mediterranean climate, measuring  $\delta^{18}\text{O}$  and  $\delta\text{D}$  in the soil–plant–atmosphere continuum. Evidence for hydraulic lift was substantiated by the daily fluctuations observed in  $\Psi_s$  at 0.4 and 1 m depth and supported by similar  $\delta^{18}\text{O}$  values found in tree xylem sap, soil water in the rhizosphere and groundwater. From 0.25 m down to a depth of 1 m,  $\delta\text{D}$  trends differed according to vegetation type, showing a more depleted value in soil water collected under the evergreen trees ( $-47\text{‰}$ ) than under dead grasses ( $-35\text{‰}$ ). The hypothesis of a fractionation process occurring in the soil due to diffusion of water vapour in the dry soil is proposed to explain the more depleted soil  $\delta\text{D}$  signature observed under trees. Hydraulically lifted water was estimated to account for 17–81% of the water used during the following day by tree transpiration at the peak of the drought season, i.e., 0.1–14 L tree<sup>-1</sup> day<sup>-1</sup>. Significant relationships found between xylem sap isotopic composition and leaf water potential in early September emphasized the positive impact of the redistribution of groundwater in the rhizosphere on tree water status.

**Abbreviations:** hydraulic lift – (HL); leaf water potential – ( $\Psi_L$ ); soil temperature – ( $T_s$ ); soil water content – (SWC); soil water potential – ( $\Psi_s$ ); vapour pressure deficit – (VPD); tree transpiration – (E)

### Introduction

Cork-oak (*Quercus suber* L.) is a western Mediterranean evergreen oak tree. In the Iberian Peninsula they occur mostly in savannah-type formations (“montados” in Portuguese also known as “dehesas” in Spain) with a sparse tree cover, which cork-oak shares with other

evergreen oaks, mainly Portuguese holm-oak (*Quercus rotundifolia* Lam.) (Joffre et al., 1999). The regional climate is typically Mediterranean with long, hot and dry summers with mild, rainy winters. In Portugal, cork-oak woodlands cover an area of approximately 1.2 Mha largely in critical parts of the country regarding water availability (average annual rainfall of 500–650 mm) (Pereira and Fonseca, 2003). Moreover, the future climate scenario for the Iberian Peninsula according to the Hadley Centre Regional Climate

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Model, suggests that the climate under a CO<sub>2</sub> concentration in the atmosphere twice that of the present, may become substantially warmer in winter with a longer dry season than at present (Miranda et al., 2002). Indeed, the climate in Portugal has been warming during the last quarter of the 20th century with an observed increase in the frequency of dry years (Miranda et al., 2002). The putative increase in the length of the dry season may lead to severe water deficits and tree mortality. This may jeopardise the sustainability of the land use based on the “montado” and have a serious impact on its biodiversity and the associated economy. Indeed, Portugal is responsible for 54% of the world cork production, representing 1.4% of the gross domestic product (Mendes, 1998).

In these seasonally water-limited ecosystems, the different length of biological activity cycles of different plant functional groups and the stratification of soil water and root systems are key factors to insure community composition (Lin et al., 1996). One important feature of trees in such environments is deep rooting (Canadell et al., 1996). For example, in a Portuguese holm-oak “montado” it was observed that some trees could tap the groundwater table at approximately 13 m below soil surface in summer (David et al., 2004). Under these conditions, hydraulic lift (HL), a passive mechanism driven by a water potential gradient that transfers water through the root system, from the deep moist soil to the shallower soil, is likely to occur (Mooney et al., 1980; Richards and Caldwell, 1987). This mechanism occurring during the night at low transpiration rate provides temporary stored water to the upper soil layers around the plant, which is rapidly extracted during the following morning by the roots of plants performing HL as well as of neighbouring plants with shallower root systems. It has been shown that HL can substantially increase plant transpiration in the following day and thus significantly contribute to ecosystem evapotranspiration (Caldwell et al., 1998; Dawson, 1993a). Several studies reviewed by Jackson et al. (2000), have highlighted the occurrence of this process in some Mediterranean plant species. To our knowledge it does not seem that the mechanism has yet been described for the European *Quercus suber*.

In recent years, water uptake by plants (Dambrinne et al., 1993; Ehleringer and Dawson,

1992; Kolb et al., 1997) as well as HL (Dawson, 1993a; Peñuelas and Filella, 2003; Ryel et al., 2003; Sekiya and Yano, 2004) have been investigated using hydrogen ( $\delta D$ ) and oxygen isotope ratio ( $\delta^{18}O$ ) analyses in xylem and soil water. In the case that no isotopic fractionation occurs during water uptake and transport from the roots to the twigs as stated by Washburn and Smith (1934), the stable isotope ratios  $\delta D$  and  $\delta^{18}O$  in the xylem sap should be identical to that of soil water at the specific depth in the profile where it is taken up by roots (Dawson and Ehleringer, 1993). Hydrogen and oxygen isotope analyses have been successfully used to determine the dependence of a species on shallow or deep soil water (Dawson, 1993a; White et al., 1985; Williams and Ehleringer, 2000). The same method was used to follow changes in the zone of water uptake over time when soil moisture at different depths varies with season (Dawson, 1998; Ehleringer et al., 1991; Lin et al., 1996).

In this work we studied the water sources for young cork-oak (*Quercus suber*) trees during the drought period (June–September) in southern Portugal in order to improve our understanding of vegetation water use and tree adaptation to summer drought. The aim of the study was to identify cork-oak water uptake patterns by measuring  $\delta D$  and  $\delta^{18}O$  in groundwater, soil water at different depths and xylem water. The possible occurrence of hydraulic lift was hypothesised and tested through a series of continuous soil water potential measurements near the surface and comparing these with water uptake patterns. We tested also the hypotheses that trees having better access to groundwater or performing HL would present the best water status and that HL is a quantitatively important process in the local water balance.

## Material and methods

### *Experimental site*

The study took place in Herdade da Mitra (N 38°31.664', W 8°01.380', 221 m altitude) 12 km southwest of Évora in southern Portugal. The experimental site is characterized by a Mediterranean mesothermic humid climate with hot and dry summers (Reis and Gonçalves, 1987).

Precipitation (ARG100 rain gauge, EM Ltd., Sunderland, UK), air humidity (Fischer 431402 sensor, K. Fischer GmbH, Drebach, Germany), and temperature from  $-0.8$  m depth up to 2 m height (Thermistor M841, Siemens, Munich, Germany) were continuously recorded by a datalogger (DL2e, Delta-T Devices Ltd., Cambridge, UK) based on Coordinated Universal Time/Greenwich Mean Time and set up at the field site. Daily precipitation, daily mean air temperature, and daily vapour pressure deficit (VPD) were recorded during 2003.

The experimental plot is on an acid Litholic non-Humic soil derived from Gneiss with a pH of 4–6 (David, 2000), on a 5% slope. A small river stands 20 m from the lower part of the experimental area. A 25 m depth borehole was drilled 500 m away from the experimental area, from which the soil and geological profiles were analysed (David, 2000) as shown on Figure 1. From the surface to 1 m depth, the soil was constituted by 88.9% of sand, 4.9% of silt, and 6.3% of clay, with a low water retention capacity of 5% ( $pF_{2.5}=8$  and  $pF_{4.2}=3$ ).

The experimental plot encompasses an area of 0.264 ha ( $46\text{ m} \times 60\text{ m}$ ) covered with *Quercus suber* L. trees planted in 1988, with an understorey mainly composed of *Cistus salviifolius* L.

and *C. crispus* L., and herbaceous plants (mostly winter-spring C3 annuals), which life cycle usually ended in late June. Inside the plot, there were 75 *Quercus suber* trees with a diameter at breast height (DBH) varying between 0.10 and 0.21 m and a height greater than 4.5 m. A sample of 27 trees was selected for ecophysiological measurements, with representative mean DBH and height of 0.12 m ( $SE \pm 0.6$ ) and 5.3 m ( $SE \pm 0.2$ ), respectively.

#### Leaf water potential

Leaf water potential ( $\Psi_L$ ) was measured with a pressure chamber (PMS 1000, PMS Instruments, Corvallis, OR, USA) (Scholander et al., 1965) on 3 sun-exposed leaves of each of the 27 sampled trees. Diurnal courses of  $\Psi_L$  were measured at predawn (5:00), in the mid morning (10:00), at midday (13:00), in the mid afternoon (16:00) and in the evening (19:00), in late June and early September.

#### Tree transpiration

Sap flow (F) was monitored continuously with sap flux density measurements using the thermal dissipation method (Granier, 1985, 1987) from

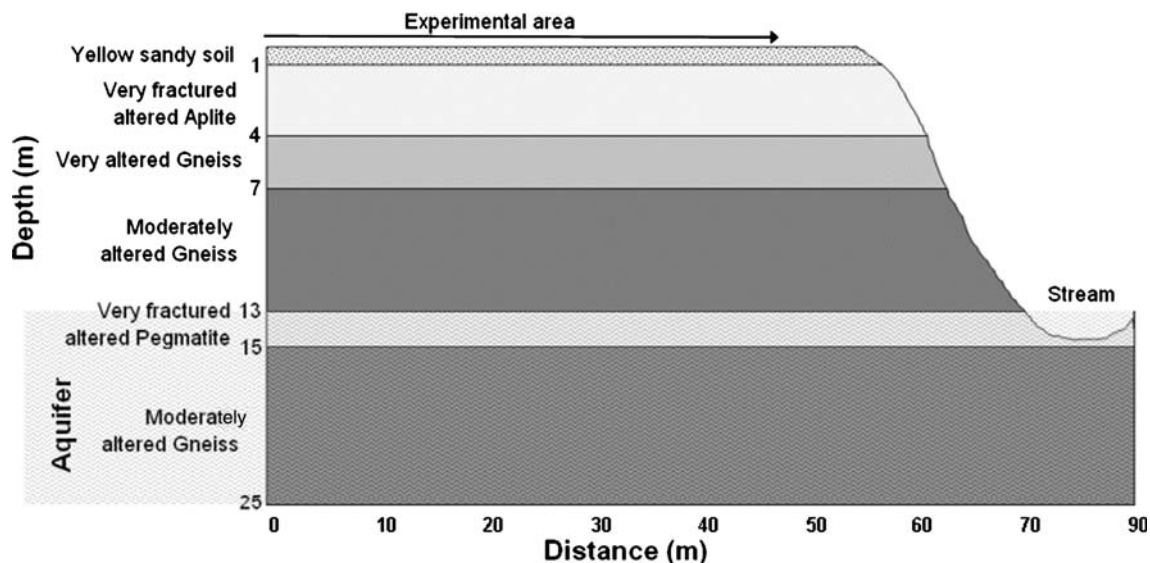


Figure 1. Schematic representation of the hydrogeological profile of the experimental area (David, 2000). The arrow indicates the direction of slope and the position of the stand, grey wave symbol indicates the location of the groundwater aquifer.

July 2003 to October 2004. One sensor (UP GmbH, Landshut, Germany) was radially inserted into the xylem on the North face of the trunk of 22 of the 27 selected trees. A detailed description of the sensors and sap flow calculation can be found in David et al. (2004). All sensors were connected to DL2e datalogger (Delta-T Devices Ltd., Cambridge, UK) measuring sap flow every minute and recording 30 min averages. Tree transpiration (E) was considered equal to sap flow (F) for daily totals and was expressed in  $L\ tree^{-1}\ day^{-1}$  or  $L\ m^{-2}\ day$ , per unit of crown-projected area.

#### *Soil water potential*

Soil water potential ( $\Psi_s$ ) was monitored using equitensimeters (EQ 15, Ecomatik GmbH, Dachau, Germany) under the canopy of five trees (A11, A12, A13, D6 and D22). The sensors were installed using an auger hole, refilled after sensor installation. Two sensors were installed at 0.4 and 1 m depths in the soil, on the north facing side, 1–1.5 m away from the stem base of each sample tree. Each sensor was individually calibrated for matric potential ranging from 0 to  $-1.5\ MPa \pm 0.005\ MPa$ . This could however be extrapolated to  $-2.5\ MPa$ , since EQ15 sensors show a linear output between  $-1.5$  and  $-2.5\ MPa$ , as detailed by the manufacturer (pers. comm. Dr. Jinchun Liu). During installation, care was taken to ensure minimal disturbance to the soil. Data were measured every 5 min, and half hourly averaged values were stored in a datalogger protected from solar radiation and heat gradients.

#### *Soil sampling*

Soil samples were collected for mass spectrometry analysis of soil water and for soil volumetric water content determination. Three soil profiles were sampled on the 17th of August, on a vertical transect along the plot: in the vicinity of large trees (height  $> 4\ m$ ) towards the river; under small trees (height  $< 1\ m$ ) in the middle of the plot; amongst dead grasses, where no trees were present, and in the upper reaches of the plot. From these profiles, samples were collected every 0.1 m from the surface down to 0.6 or 1 m depth. The presence of large Aplite and Gneiss rocks

(diameter  $> 0.4\ m$ ) below 1 m depth did not allow the collection of deeper samples (Figure 1).

#### *Soil volumetric water content*

Soil volumetric water content (SWC) was measured on sub-samples of soil cores extracted for mass spectrometry analysis of soil water. SWC was measured gravimetrically evaporating water from 10 g soil sub-samples at  $105^\circ C$  for 24 h, and measuring the remaining soil mass after cooling in a desiccator. The apparent density of the soil was calculated measuring the volume obtained by adding 10 mL of water to 5–10 g of dry soil in a graduated oil-can. A linear relationship ( $r^2 = 0.89$ ,  $n = 111$ ) was obtained between soil dry mass and soil apparent volume, with slope representing the mass of dry soil per unit volume, i.e. soil bulk density ( $\rho_s$ ). The mean  $\rho_s$  measured on 111 soil samples was  $0.434\ g\ cm^{-3}$  with a standard deviation of 0.035. The soil volumetric water content was obtained by multiplying the mass of water by  $\rho_s$ .

#### *Soil root biomass and diameter*

In order to quantify the tree root biomass and distribution a 4 m long \*1 m wide \*1.4 m deep pit was dug parallel to two large trees ( $> 4\ m$  height), at a distance of 1.5 m from the base of the trunk, and of 40 m from the stream. From this pit, 3 soil profiles were collected along the pit transect from which 10 soil samples were collected vertically every 0.1 m from the surface to 1 m depth using coring tubes of 3.7 cm of internal diameter and 20 cm length. In the laboratory, roots were extracted manually, washed and dried in the oven at  $65\ ^\circ C$ , weighted and scanned using Epson Expression 1600 with 1600 dpi, 3.6 Dmax optical density with Epson Expression Transparency unit B813182. Root diameter was calculated from digital pictures using WinRHIZO Pro v.2003b program from Regent Instruments Inc. (Sainte-Foy, Quebec, Canada).

#### *Stable isotope sampling*

Two lignified twigs were sampled on each of the 27 selected trees at 10 cm from the nearest leaves. The sampling took place at midday before (26th June) and at the end of the summer

drought (16th September), afterwards minimum predawn  $\Psi_L$  was observed. Rainfall samples were collected once a month using a decantation flask filled with a layer of liquid paraffin provided with a funnel. Groundwater samples were collected on a monthly basis in three wells 500 m and 3 km away from the plot, at 13 m and 5 m depths respectively. Since river water could be a possible water source for the trees, stream water was collected in June before the river dried out, to compare its isotopic signature with that of twig xylem water. All water, mineral and organic samples were collected in plastic test tubes closed with plastic stoppers and hermetically sealed with parafilm to avoid any alteration of the isotopic signature due to evaporation. Samples were kept in the freezer ( $-18\text{ }^\circ\text{C}$ ) until water extraction and mass spectrometry analyses were performed.

#### *Xylem water extraction and mass spectrometry analysis*

Water was extracted from samples by cryodistillation as detailed in Otieno et al. (in press).

One microliter of extracted water 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  $\text{H}_2$  and  $\text{CO}$ . These gases were then analysed for their  $^{18}\text{O}/^{16}\text{O}$  and  $^2\text{H}/^1\text{H}$  isotope ratio with an Isotope Ratio Mass spectrometer (IRMS) Delta Plus XL (Finnigan, Bremen Germany).  $\delta^{18}\text{O}$  isotope ratio was determined from the time integrals of the peak areas of the ion intensities  $m/z$  30 and 28.  $\delta^{18}\text{O}$  is defined as the relative deviation of the  $^{18}\text{O}/^{16}\text{O}$  ratio of the sample from the international standard VSMOW. In a similar way,  $\delta\text{D}$  was determined from  $m/z$  3 and 2 and referenced to VSMOW. For more details see Saurer et al. (1998).

$\delta^{18}\text{O}$  and  $\delta\text{D}$  values were expressed in parts per thousand (‰) and defined as:

$$\delta = (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 1000 \quad (1)$$

Where  $R_{\text{sample}}$  is the isotope ratio  $^{18}\text{O}/^{16}\text{O}$  or  $^2\text{H}/^1\text{H}$  of the sample and  $R_{\text{standard}}$  that of the standard.

## Results

### *Weather*

In 2003 – January through December – total rainfall at the site was 656 mm. Between May and the beginning of September precipitation was negligible. Major autumn rainfall events begun by the end of September 2003. Maximum and minimum mean air temperatures during summer 2003 were  $30.6 (\pm 6.8)$  and  $14.3 (\pm 3.4)$   $^\circ\text{C}$ , respectively. Highest temperature recorded during this period was  $45.8\text{ }^\circ\text{C}$  and occurred in August. On most of the days of summer 2003, dew formation occurred between 6:00 am and 7:00 am (i.e.  $\text{VPD} = 0$ ).  $\text{VPD}$  was maximum in August reaching 4300 Pa and declined significantly with the onset of autumn rains and remained low thereafter with maximum averaging 500 Pa and minimum reaching 14 Pa in December.

### *Seasonal variations of precipitation and groundwater isotopic signatures*

From 2002 to 2003,  $\delta^{18}\text{O}$  in precipitation water varied between  $-6.1\text{‰}$  (April 2002) and  $0.1\text{‰}$  (August 2002) (Figure 2a). Over the same period, minimum and maximum  $\delta\text{D}$  values in the precipitation were  $-40.3\text{‰}$  in April 2002 and  $-6.7\text{‰}$  in August 2002, respectively, representing a variation of  $33.6\text{‰}$  (Figure 2b). The seasonal variation of groundwater isotopic composition was smaller, with  $\delta\text{D}$  values ranging between  $-34.3\text{‰}$  (April 2002) and  $-4.1\text{‰}$  (October 2002), and  $\delta^{18}\text{O}$  values between  $-5.4\text{‰}$  (June 2003) and  $-2.3\text{‰}$  (October 2002) (Figure 2a, b). There was a significant correlation between  $\delta^{18}\text{O}$  and  $\delta\text{D}$  in precipitation water ( $r^2 = 0.76$ ,  $P < 0.0001$ ,  $n = 30$ ). This relationship, also called Local Meteoric Water Line (LMWL), was best described under our climatic conditions by the equation  $\delta\text{D} = 6.19 (\text{SE} \pm 0.66) * \delta^{18}\text{O} - 2.14 (\text{SE} \pm 2.62)$ . The LMWL had a slightly lower slope and lower  $d$ -excess value compared to the global meteoric water line ( $\delta\text{D} = 8 * \delta^{18}\text{O} + 10$ ) (Craig, 1961). The isotopic composition of rainfall followed a seasonal course. The most positive  $\delta^{18}\text{O}$  and  $\delta\text{D}$  values of precipitation water were found during the summer, when hardly any precipitation occurred (Figure 2). The average  $\delta^{18}\text{O}$  and  $\delta\text{D}$  values in precipitation were respectively  $-22.30 \pm 2.94\text{‰}$  and  $-3.15 \pm 0.50\text{‰}$  over the

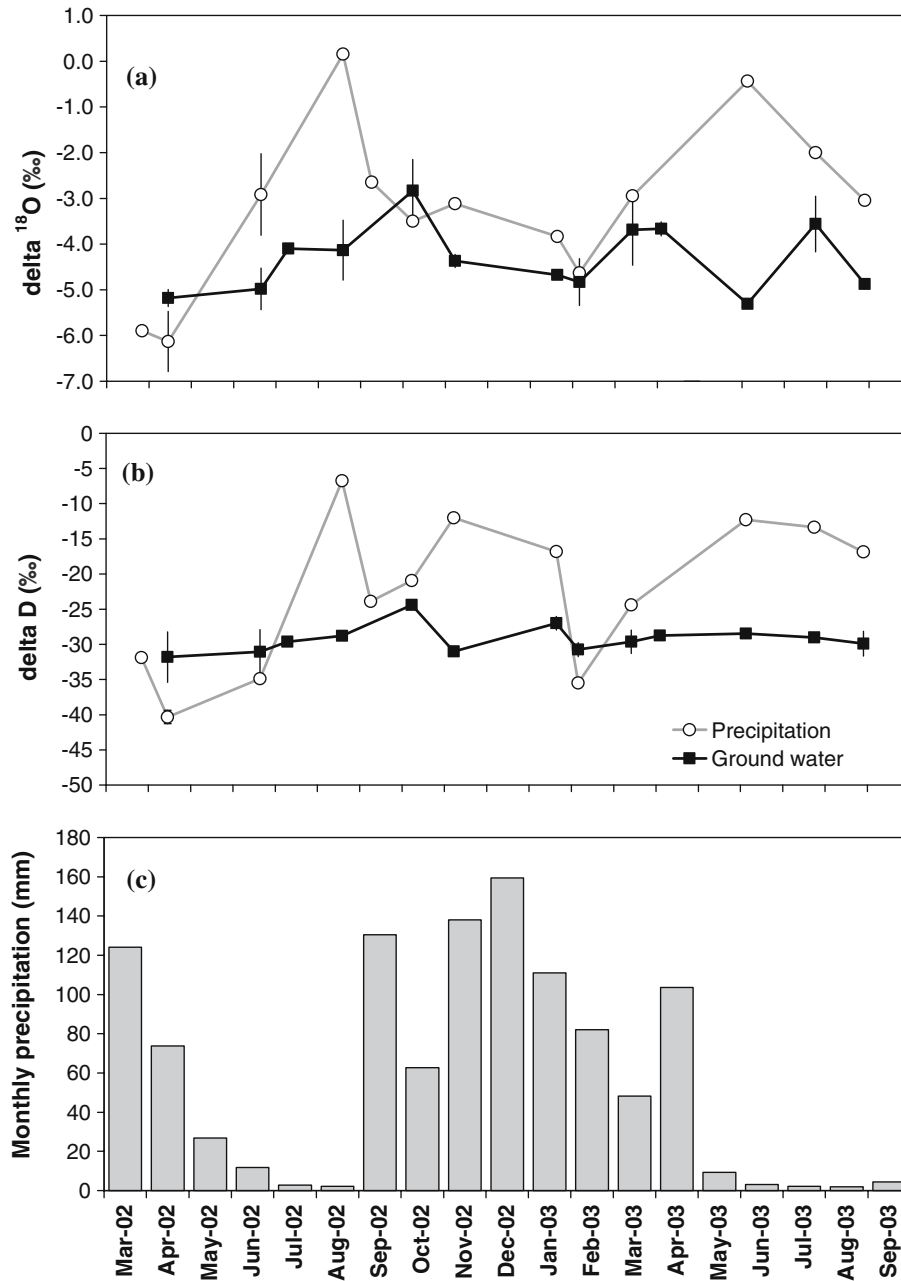


Figure 2. Seasonal variation of  $\delta^{18}\text{O}$  (a) and  $\delta\text{D}$  (b) in precipitation (open circles) and groundwater (filled squares), and monthly precipitation (c) from March 2002 to September 2003.

2-year study period. The relatively high values of  $\delta\text{D}$  and  $\delta^{18}\text{O}$  observed in precipitation compared to the global observations can be explained by the short distance of the experimental site from the Atlantic Ocean (~80 km) (Dansgard, 1964; Tani-gushi et al., 2001). The average of  $\delta^{18}\text{O}$  and  $\delta\text{D}$

values in precipitation were more positive than mean groundwater ( $\delta^{18}\text{O} = -29.79 \pm 0.40\text{‰}$ ,  $\delta\text{D} = -4.39 \pm 0.14\text{‰}$ ) over the 2-year study period. These differences could also be due to interception of more positive water by plant uptake during summer in the surface soil layers, and also

because groundwater recharge mainly happens between October and December, when more depleted rainfalls occur (DeWalle et al., 1997).

### Tree transpiration

Tree transpiration ( $E$ ) varied from 0.5 to 17.6 L tree<sup>-1</sup> day<sup>-1</sup> over the summer period, with a daily average reaching  $\sim 5 \pm 0.9$  L tree<sup>-1</sup> day<sup>-1</sup> or  $\sim 1 \pm 0.2$  L m<sup>-2</sup> day<sup>-1</sup> on a crown-projected area basis (Table 1). On the experimental plot of 2400 m<sup>2</sup>, there was a total of 475 trees with a DBH ranging from 1 to 21 cm. From the monthly linear regressions obtained between DBH and tree transpiration from April to August, we calculated the total average tree transpiration from the plot ( $E_{\text{canopy}}$ ) as 0.33, 0.59, 0.84, 0.39 and 0.35 mm day<sup>-1</sup> in April, May, June, July and August, respectively, on a ground area basis. The last significant rainfall events before soil sampling (17th August) occurred on 22nd April (15 mm) and 5th May (9 mm). Therefore, cumulative tree transpiration from the plot was 64 and 58 mm, from the 22nd of April to the 17th of August, and from the 5th of May to the 17th of August, respectively.

### Seasonal changes in soil water potential

Soil water potential  $\Psi_s$  measured under five trees decreased significantly from spring to summer, with the lowest mean values of  $-2.5$  and  $-2.0$  MPa recorded at 0.4 m and 1 m depths, respectively, at the beginning of September (Figure 3). The  $\Psi_s$  at 0.4 m depth decreased rapidly between May and July. Differences in moisture decline of the topsoil could be attributed to differences in competition for water resources, since

crown sizes and vegetation densities were not even. After July the decline in  $\Psi_s$  at the 0.4 m depth was slow and uniform around 4 of the 5 studied trees, but remained steep for tree A11. It returned to zero after a strong rain event (31 mm) at the end of September (Figure 3). The earlier return to zero in  $\Psi_s$  under tree A11 could be explained by the proximity of the datalogger shed, which might have collected and redistributed a higher rain amount to this tree.

The fact that  $\Psi_s$  remained close to 0 MPa until late June at 1 m depth can be explained by the absence of root water absorption, the SWC remaining at field capacity (Figure 3). In July, differences among trees began to appear when roots began to absorb water at this depth (Figure 3). The different time lags and rates of decline in  $\Psi_s$  that were observed at this depth among the five trees could be attributed to differences in rooting depth. At 1 m depth  $\Psi_s$  did not respond to short rainfall events such as those that occurred at the end of August (27th, 28th and 31st, with respectively 1.4, 0.6 and 4.4 mm), and did not immediately return to zero after the stronger rainfall event at the end of September.

### Daily fluctuations of soil water potential

Daily fluctuations could be observed in  $\Psi_s$  at 0.4 m depth, beginning in mid June, with increasing amplitude until mid September. By then, the  $\Psi_s$  increase during the night was maximal in all locations (Figure 3). The magnitude of nocturnal  $\Psi_s$  increase was minimal in the soil around tree D22 (0.02 MPa) and maximal around tree A11 (ca. 0.15 MPa), trees A12, A13 and D6 showing intermediate values (0.04–0.10 MPa). Daily fluctuations were higher at 0.4 m depth as compared to 1 m depth.

Table 1. Tree daily minimum, maximum and average transpiration observed on 22 of the 27 selected trees during the drought period of 2003, expressed by tree (L tree<sup>-1</sup> day<sup>-1</sup>) and by projected crown area (L m<sup>-2</sup> day<sup>-1</sup>)

	$n$	$E$ (L tree <sup>-1</sup> day <sup>-1</sup> )				$E_{\text{pca}}$ (L m <sup>-2</sup> day <sup>-1</sup> )			
		Min	Max	Mean	SE	Min	Max	Mean	SE
July	22	0.93	16.85	5.64	0.99	0.15	4.20	1.26	0.23
August	22	1.11	17.62	4.87	0.91	0.21	4.63	1.09	0.22
September	22	0.52	15.27	4.03	0.76	0.10	4.02	0.91	0.19

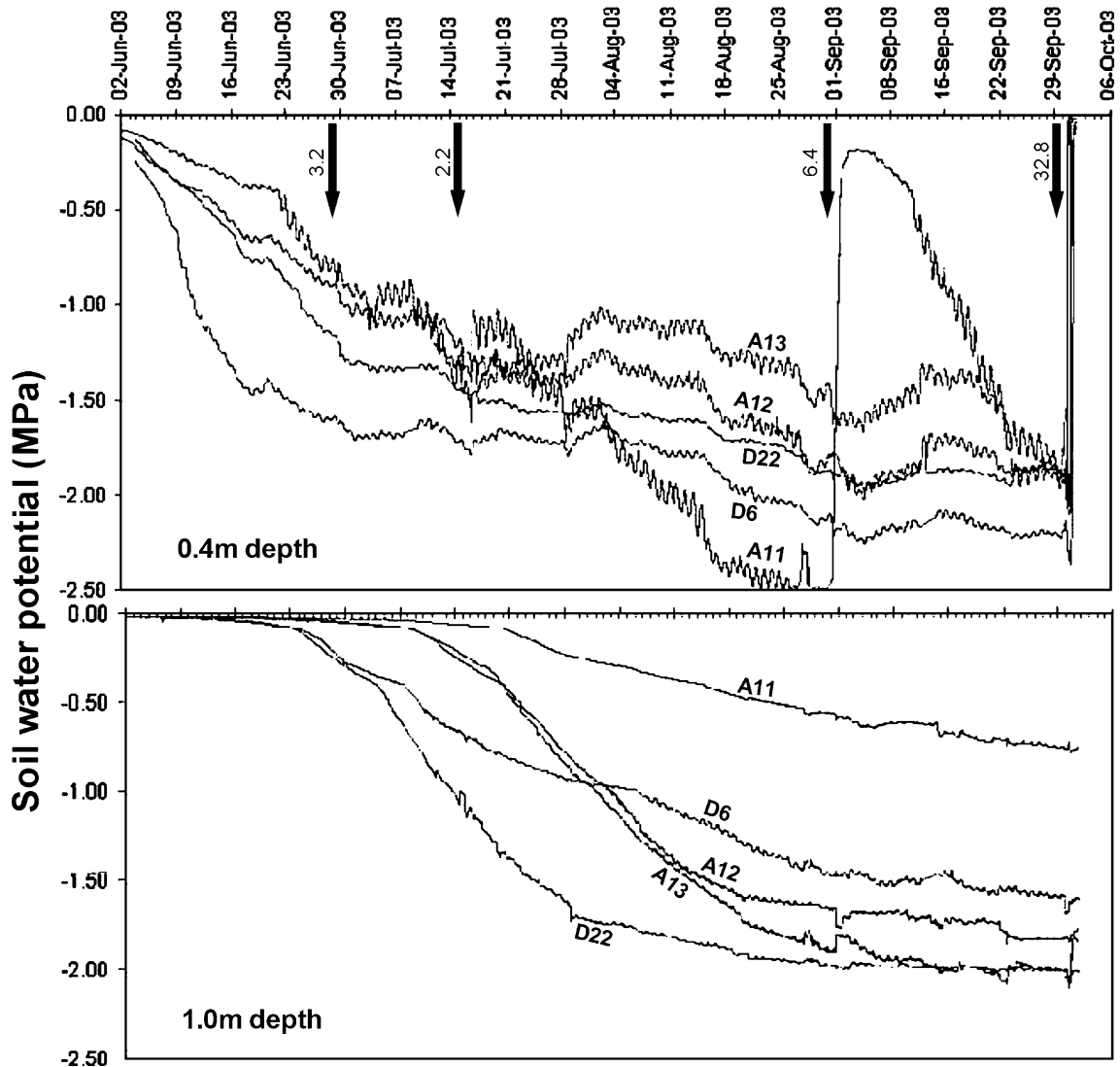


Figure 3. Soil water potential ( $\Psi_s$ ) measured half hourly at 0.4 m and 1 m depths for the study stand of *Q. suber*, measured around 5 main trees, A11, A12, A13, D6 and D22 during summer 2003. Measurements of tree A11 began on the second week of July. Modified from Otieno et al. (In press). Arrows indicate rainfall events and the amount of water (mm).

Figure 4 shows the variation in  $\Psi_s$  and soil temperature ( $T_s$ ) at 0.4 m depth around tree D6 during one week in mid August. Every day,  $\Psi_s$  stopped decreasing few hours before night (around 18:00) and increased during night time (20:30) until the following sunrise (6:40), when  $\Psi_s$  began to decrease again. At 0.4 m depth,  $T_s$  also showed daily fluctuations with increases occurring during the day from 10:30 to 20:30, and decreases occurring during the night from 21:00 to 10:00 (Figure 4). Since the daily fluctuations in  $T_s$  were

not in phase with soil  $\Psi_s$  at 0.4 m depth as indicated in Figure 4 we exclude a temperature sensitivity on the equitensiometer voltage output or consider it to be minimal, even at shallower soil depths where higher temperature fluctuations are observed. Also the amplitude of temperature fluctuations remained constant from the 7th to 15th of August, whereas night  $\Psi_s$  variation progressively increased from 0.02 to 0.03 MPa over the same period. These results show that  $T_s$  was not likely to have affected equitensiometer measurements.



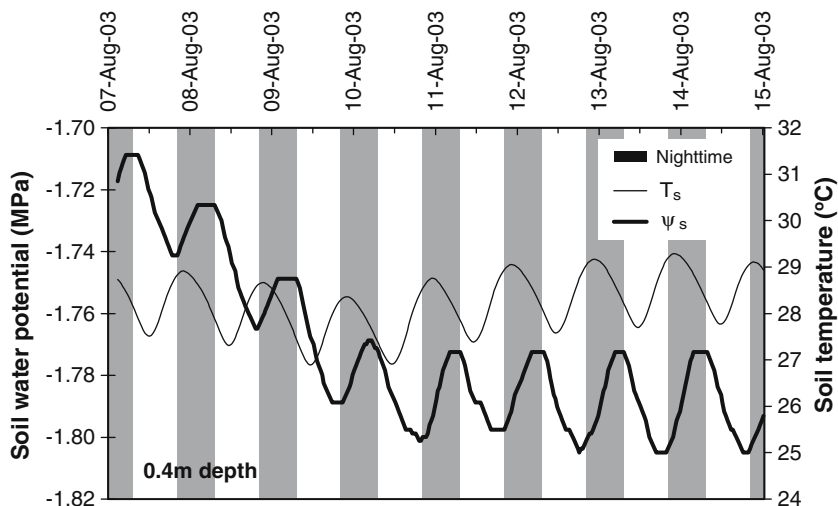


Figure 4. Time course of soil water potential ( $\Psi_s$ ; bold curve) measured at 0.4 m depth under *Q. suber* tree (D6) showing hydraulic lift. Nighttime was occurring between 20:30 and 6:40 (shaded areas). Soil temperature ( $T_s$ ; thin curve) is represented to show that equitensimeters did not respond to temperature changes.

#### Soil volumetric water content

The SWC measured on soil profiles collected in late August under the three vegetation types is shown in Figure 5. The SWC increased with depth, from 2% on the topsoil to ~4% at 0.3 m depth, independent of the vegetation cover, which was attributed to water evaporation due to high temperature and VPD and lack of precipitation. Larger differences in SWC were found below the 0.3 m depth, depending on the vegetation type: under dead grasses SWC increased to a maximum of 12% at 0.9 m depth; under small trees it increased slightly up to 0.35 m and then remained constant down to 1 m; and under large trees it decreased to 3% at 0.6 m depth. Differences in SWC were expected to depend on the distance of the soil profiles to the river, with higher values close to the river and thus near the large trees. On the contrary higher moisture contents were found under dead grasses, in the profile furthest from the river (Figure 5).

#### Root biomass

The total mean root biomass with a diameter less than 0.5 mm measured between the surface and 1 m depth was  $3.70 \pm 0.06 \text{ kg m}^{-3}$ . The largest amount of fine roots was observed in the top soil

at 0.2 m depth ( $0.70 \pm 0.3 \text{ kg m}^{-3}$ ), representing  $18.9 \pm 8.5\%$  of the total root biomass (Figure 6a). In deeper layers, the largest root amounts were observed at 0.4 and 0.9 m depth with  $0.47 \pm 0.14$  and  $0.63 \pm 0.32 \text{ kg m}^{-3}$  respectively, representing  $12.8 \pm 4.0$  and  $17.0 \pm 8.6\%$

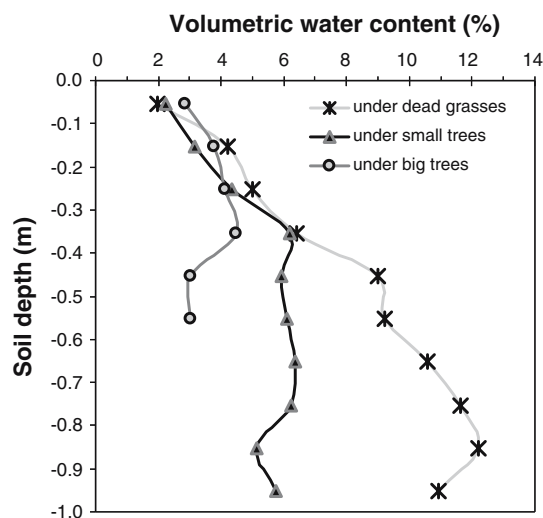


Figure 5. Volumetric soil water content of the three soil profiles collected under dead grasses, small trees (<1 m height) and big trees (>4 m height), versus depth, in late August 2003.

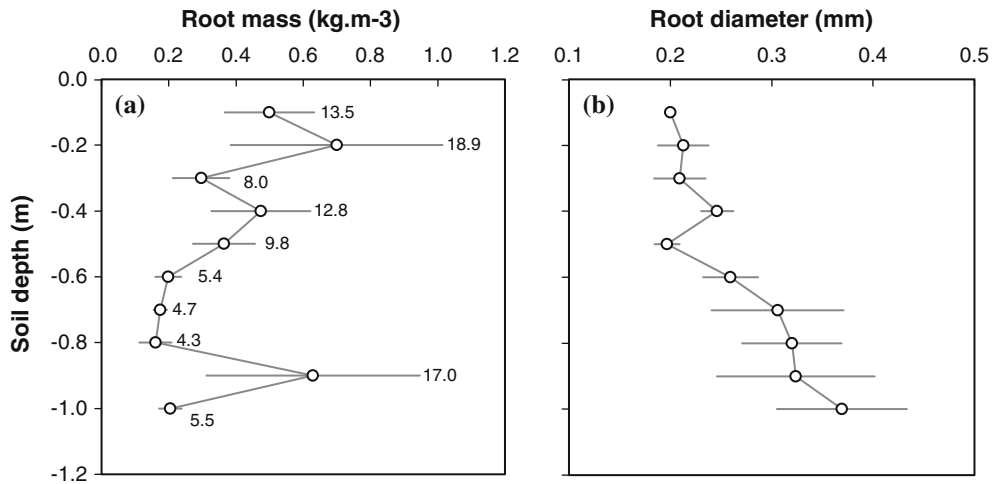


Figure 6. Average root biomass (a) and diameter (b) for  $0 < \text{root diameter} < 0.5$  mm as a function of soil depth ( $n=3$ ). Error bar represents the standard error of the mean. Values above each bar are percentages of root biomass of the total biomass measured down to 1 m depth.

of the total root biomass until 1 m depth. The mean root diameter increased with depth, varying from  $0.20 \pm 0.003$  mm on the top soil to  $0.37 \pm 0.06$  mm at 1 m depth (Figure 6b). Along the transect, larger roots ( $> 2$  mm) were clearly more concentrated between 0.3 and 0.5 m depth, and between 0.9 and 1 m depth. The number of root tips decreased from 0.5 to 0.9 m depth. However, rare larger root tips ( $> 5$  mm) could still be observed until 1.4 m depth, the lowest assessed depth.

#### Soil water isotopic composition

Soil water  $\delta^{18}\text{O}$  values showed similar trends under large and small trees from 0.15 m down to 0.55 m depth, with a decrease in the isotopic composition from 3.5 to  $-6\text{‰}$ , respectively at the peak of drought (Figure 7a). From 0.55 m depth down to 0.85 m the soil water became progressively more depleted with  $\delta^{18}\text{O}$  decreasing to  $-7\text{‰}$ . In soil collected under dead grass, however,  $\delta^{18}\text{O}$  was in average  $2\text{‰}$  more positive between 0.35 m depth and 0.65 m depth compared to soil collected under trees. In the topsoil, there was a high variability of water isotopic signature, values ranging from  $0.5\text{‰}$  under small trees to  $3.5\text{‰}$  under big trees. The variability disappeared at 0.15 m depth, with

$\delta^{18}\text{O}$  around  $2.5\text{‰}$ . The high variability observed in the topsoil compared to 0.15 m depth was attributed to spatial variability of dew deposition on soil.

Soil water  $\delta\text{D}$  values showed a trend similar to  $\delta^{18}\text{O}$  under all vegetation types down to 0.25 m, with a  $\sim 8\text{‰}$  enrichment from 0.05 to 0.15 m followed by an 8–12‰ depletion until 0.25 m depth (Figure 7b). Isotopic enrichment can be expected in the upper soil horizons in the summer due to high evaporation rates. However, soil water at 0.05 m depth was depleted compared to 0.15 m depth. As observed for  $\delta^{18}\text{O}$ , this depletion could be explained by dew deposition on the topsoil. This hypothesis of dew deposition was supported by VPD values around zero measured between 6:00 and 7:00 during most of the summer days. From 0.25 m down to 1 m depth,  $\delta\text{D}$  trends differed with vegetation type, showing more depleted values for soil water collected under trees ( $-47\text{‰}$ ) than under dead grasses ( $-35\text{‰}$ ) (Figure 7b). Also, the soil water deuterium signature at 0.5 m depth under the trees ( $-47\text{‰}$ ) was more negative than that of groundwater ( $-31 \pm 3\text{‰}$ ) and precipitation ( $-23 \pm 3\text{‰}$ ) (Figure 7b, d), and even more negative than the most negative  $\delta\text{D}$  value observed in rainfalls collected in April 2002 ( $-40\text{‰}$ ) and in January 2003 ( $-35\text{‰}$ ), respectively (Figure 2a).

*Comparison of isotopic signature in xylem water and other compartments*

Three different water sources were available for the trees in the experimental area: (1) rainfall, which was separated into winter (September 2002–May 2003) and summer precipitation (May–September 2003) in order to distinguish potential use of summer precipitation by trees during the drought period; (2) groundwater, which can be reached by deep rooting and (3) stream water, due to the presence of a small river in the vicinity of the experimental plot (~20 m). Stream water samples were collected in June, before the river dried out. The deuterium and the

oxygen signatures of the stream water ( $-19.2\text{‰}$  and  $-1.9\text{‰}$ , respectively) were both less negative than soil water signature at the rooting depth ( $\delta D = -43$  to  $-47\text{‰}$  and  $\delta^{18}\text{O} = -2$  to  $-6\text{‰}$ ) and than tree xylem water ( $\delta D = -38.1\text{‰}$  and  $\delta^{18}\text{O} = -4.22\text{‰}$ ) (Figure 7). No significant differences in deuterium signature of xylem water were found between June and September (Figure 7d). There was a significant difference in  $\delta^{18}\text{O}$  xylem water between June and September. Xylem water collected in June was significantly more negative than precipitation and groundwater, whereas xylem water collected in September was only different from summer precipitation (Figure 7c).

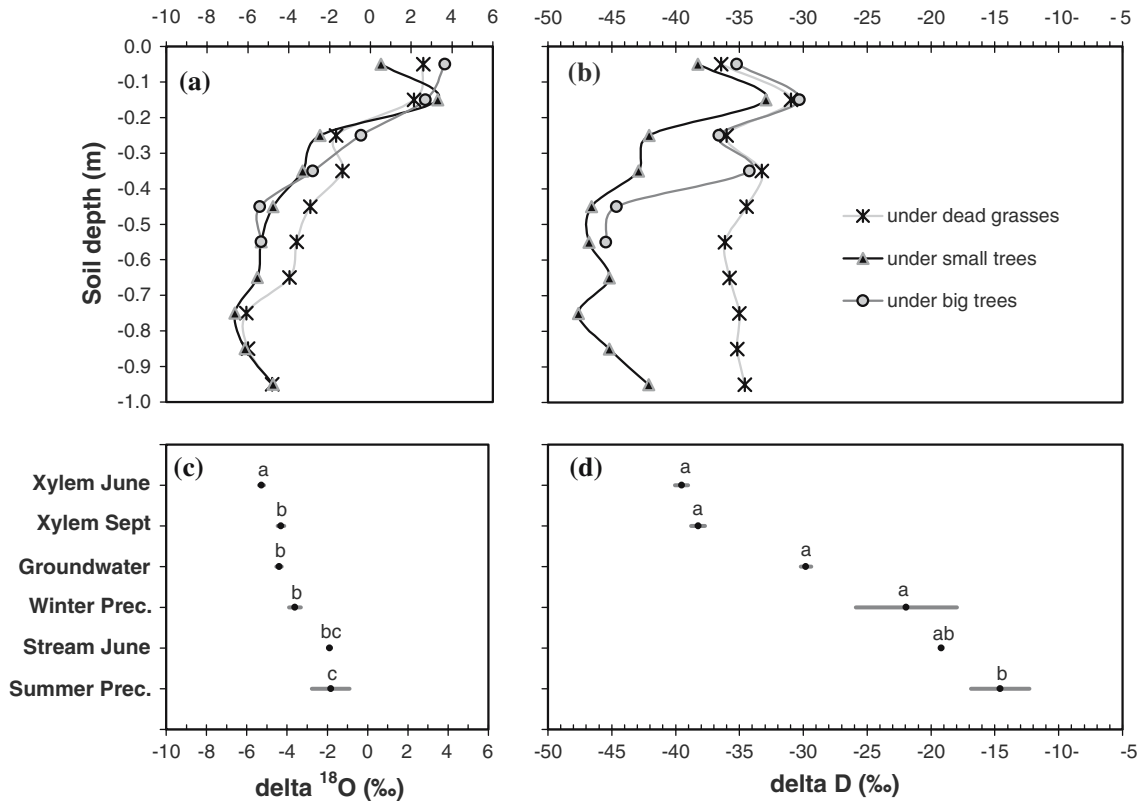


Figure 7. Soil water  $\delta^{18}\text{O}$  (a) and  $\delta D$  (b) signatures versus soil depth under big trees (circles), small trees (triangles), and dead grasses (crosses). Soil profiles were collected at the end of August 2003 at approximately 20 m from each other. Water  $\delta^{18}\text{O}$  (c) and  $\delta D$  (d) signatures in tree xylem in June 2003 ( $n=27$ ), and September 2003 ( $n=27$ ), groundwater (2002–2003,  $n=30$ ), summer precipitation (June–September 2003,  $n=3$ ), winter precipitation (October 2002–May 2003,  $n=5$ ), and stream water (June 2003,  $n=2$ ). Black circles indicate mean value. Grey error bars indicate standard errors of the means. Differences between  $\delta^{18}\text{O}$  means have been tested with One-Way ANOVA (letters indicate significant differences between means according to Newmann–Keuls’s test), and since the homocedasticity test failed,  $\delta D$  means have been tested using One-Way ANOVA on ranks (small caps letters indicating significant differences between means according to Dunn’s test). Part of  $\delta^{18}\text{O}$  data was modified from Otieno et al. (In press).

Table 2. Comparison between June and September 2003 of the relationship linking  $\Psi_L$  and twig xylem isotopic signature ( $n=26$ )

$\Psi_L$	Time	$\delta^{18}\text{O}$				$\delta\text{D}$			
		June		September		June		September	
		$r^2$	$P$	$r^2$	$P$	$r^2$	$P$	$r^2$	$P$
Predawn	5:00	0.006	0.711	0.263	0.006	0.006	0.711	0.231	0.013
Morning	10:00	0.054	0.243	<b>0.508</b>	<b>&lt; 0.001</b>	0.031	0.386	0.208	0.019
Midday	13:00	0.011	0.602	0.15	0.046	0.031	0.386	0.094	0.128
Afternoon	16:00	0.003	0.771	0.314	0.002	0.007	0.681	0.135	0.0645
Evening	19:00	< 0.001	0.902	0.347	0.001	< 0.001	0.957	<b>0.287</b>	<b>0.005</b>

Shaded cells indicate the significant linear relationships ( $P < 0.05$ ). The best relationships obtained are indicated in bold characters.

### Relationship between xylem isotopic signature and $\Psi_L$

Significant negative linear relationships were observed between twig xylem isotopic composition ( $\delta^{18}\text{O}$  and  $\delta\text{D}$ ) and  $\Psi_L$  measured at different times of the day in early September. The results of the statistical tests are summarised in Table 2. The best correlations were obtained between  $\delta^{18}\text{O}$  and  $\Psi_L$  measured in morning, and between  $\delta\text{D}$  and  $\Psi_L$  measured in the evening (Table 2, Figure 8). In both cases trees, which presented the more depleted xylem water had the best water status (higher  $\Psi_L$ ). In June, no significant

relationship could be observed between twig xylem  $\delta\text{D}$  and  $\Psi_L$  (Table 2).

## Discussion

### Water sources for cork-oak trees

All the results presented in Figures 3–6 give strong evidence that trees mainly absorbed water at 0.4 and 1 m depth. The same conclusions were already proposed in a previous publication based on further evidences (Otieno et al. In press). Indeed, the decrease in soil moisture in the upper soil layer (Figure 3) is due to the combined effect of weather conditions favouring evaporation and plant transpiration in June, which is at a maximum at this time of the year. The homogeneous increase of SWC from soil surface to 0.3 m depth under the three vegetation types (Figure 5) observed in late August, suggests that the loss of water from this layer was mainly due to soil water evaporation and grass transpiration before senescence. From 0.3 m down to 1 m depth, differences observed in SWC between the different profiles may be attributed to the vegetation cover type, and to their respective transpiration rates (Figure 5). These results also agree with the marked decline of  $\Psi_s$  during the drought period (July–August, Figure 3), as well as with stable isotope data showing that the signatures of tree xylem sap corresponded to soil water signatures at 0.45 m and 1 m depth (Figure 7). Furthermore, the distribution of root biomass showed that ~22.5% of the total root biomass observed until 1 m depth was located between 0.4–0.5 and 0.9–1.0 m depth

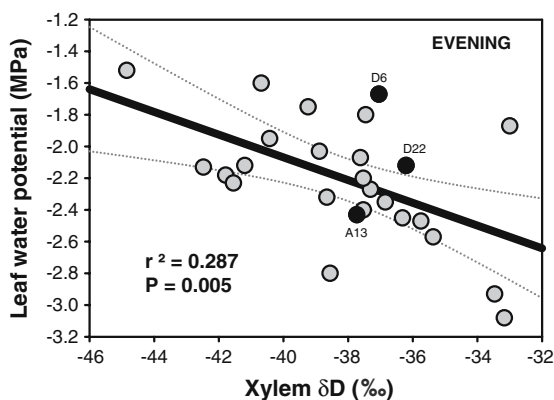


Figure 8. Best relationship obtained between evening leaf water potential (19:00) and twig xylem isotopic signature in September 2003 ( $n=26$ ). Trees D6, A13 and D22 are indicated in black as “hydraulic lifters” (samples from trees A11 and A12 were lost due to a leak during water extraction, and thus do not appear on the graphic). Trees that present more negative twig xylem signature (hydraulic lifted water) have better water status.

(Figure 6), the larger amount of roots (32.5%) found between 0 and 0.2 m depth being attributed to grass species since no difference could be observed between vegetation types in SWC until 0.3 m depth (Figure 5).

The short lag of about 2 months in the periodicity of groundwater and rainfall seasonal cycles (Figure 2a, b) shows that water moved quickly in the soil to reach 13 m depth. Also, the 2-month lag coincides with the time needed for groundwater recharge after the summer drought following first autumn rainfall events (data not shown), thus corresponding to a water infiltration velocity in soil of about  $0.2 \text{ m day}^{-1}$ . The fast movement of water in the soil thus discards the assumption of trees using old isotopically depleted water confined in the unsaturated zone.

Since the stream water was isotopically more enriched than soil water signature at the rooting depth and tree xylem water, we concluded that trees were not using stream water as a source during the summer. Also, from  $\delta^{18}\text{O}$  results, we concluded that trees were not using precipitation water from small rainfall events during the drought period (Figure 7c, d).

From the tree transpiration results, we can also conclude that by the end of summer trees were not using water stored in soil from winter/spring precipitation. Indeed, the maximum soil storage capacity between 0 and 1 m depth is about 50 mm, and cumulative tree transpiration between the latest significant spring rainfall events and soil sampling in late August exceeded this amount (more than 58 mm). Since neither the transpiration of the understorey (*Cistus* shrubs and grasses), nor the evaporation from soil surface were considered, we can assume with some confidence that soil water stored from winter/spring precipitation was already exhausted from the 0 to 1 m depth soil layer, when soil sampling took place. Therefore, the origin of soil water used by the trees at 0.4 and 1 m soil depth in late August must be different from direct late spring rainfall stored in soil.

#### *Hydraulic lift and drought adaptations in cork oak*

So far, the HL process has been described in several oak species, such as *Q. douglasii* in a Californian Mediterranean-type ecosystem (Millikin

Ishikawa and Bledsoe, 2000), *Q. incana* and *Q. laevis* in South Carolina (Espeleta et al., 2004), and *Q. agrifolia* seedlings (Querejeta et al., 2003). In our study, diel fluctuations in  $\Psi_s$  were observed under each of the five trees with equitensiometers. The amplitude of fluctuation varied from 0.02 to 0.15 MPa. Beginning in June between  $-0.2$  and  $-1.0$  MPa at 0.4 m depth, and below  $-0.5$  MPa at 1 m depth, it lasted until the lowest potential reached  $-2.5$  MPa. These observations support the occurrence of HL and are in agreement with the results obtained by Millikin (Ishikawa and Bledsoe (2000) and Ludwig et al. (2003)). They observed the same phenomenon under  $\Psi_s$  varying from  $-0.3$  to  $-3.0$  MPa under *Quercus douglasii* and  $-0.2$  to  $-5.0$  MPa under *Acacia tortilis*, respectively. Espeleta et al. (2004) also reported  $\Psi_s$  fluctuations below  $-0.2$  MPa for several species in a sandhill community, with a mean amplitude of 0.04 and 0.07 MPa for *Q. laevis* and *incana*, respectively. To our knowledge this is the first time that HL is reported in *Q. suber*.

As the  $\Psi_s$  fluctuation began in mid June, after the senescence of herbaceous plants, we concluded that the effect of HL did not have a facilitation effect on herbaceous growth. Millikin (Ishikawa and Bledsoe (2000) reached the same conclusion in Mediterranean-type oak savannah.

Occurrence of HL implies the simultaneous presence of active roots in shallow soil with low SWC and  $\Psi_s$  as well as in deep soil layers with high SWC and  $\Psi_s$ . The water potential gradient must be strong enough to allow HL to take place. The agreement between tree xylem sap  $^{18}\text{O}$  signature in September, soil water from 0.45 and 1.0 m depth and that of groundwater collected at 13 m depth (Figure 7c) suggests that cork-oak roots may reach this depth and redistributed groundwater to shallower soil layers. This result is in agreement with observations by Jackson et al. (1999), who identified taproots deeper than 10 m in *Q. fusiformis*. Also, in a recent review, the average maximum rooting depth of sclerophyllous trees, including Mediterranean oaks, was  $12.6 \pm 3.4$  m (Cana-dell et al., 1996; David et al., 2004).

The larger amplitude of  $\Psi_s$  fluctuations at 0.4 m than at 1 m indicates that a larger amount of water was redistributed at 0.4 m than at a greater depth (Figure 3). Furthermore, the mean

root diameter was lower at 0.45 m than at 0.9 m depth, for a similar root biomass (Figure 6). These observations support the conclusion that *Q. suber* had a better developed and more efficient root system at 0.4 m than at 1 m depth. We showed in a previous publication that *Q. suber* stopped growing in the middle of July when  $\Psi_s$  reached the critical value of  $-1.5$  MPa at 0.4 m depth (Otieno et al., in press) (Figure 3). Once  $\Psi_s$  reached this critical value, the source of water uptake by roots changed to deeper soil layers. The late occurrence of HL at 1 m depth, after trees have stopped above-ground growth, suggests new root formation at 1 m depth. During a long period without precipitation trees extract water from progressively deeper soil layers, following new root formation (Grieu et al., 2001; Roberts, 2000). After reaching a critical soil water threshold that could lead to vessel damage or xylem cavitation shoot elongation stops and trees invest carbon in new roots enabling them to explore deeper soil layers where there is more available water (Chaves et al., 2003).

*Deuterium fractionation and implications for the understanding of root water uptake mechanism*

Comparing  $^{18}\text{O}$  ratio in soil at different depths with tree xylem sap (Figure 7), we concluded that *Q. suber* trees were absorbing water between 0.4 and 1 m depth, in June as well as in September and that trees were performing HL, redistributing water from deeper soil layer to the main fine root system around 0.4 m and 1 m. This conclusion was also supported by the daily fluctuations in  $\Psi_s$  observed at the two depths (Figure 3). However, deuterium isotopic signature of soil water ( $-47\text{‰}$ ) was more negative than groundwater ( $-29.8 \pm 0.4\text{‰}$ ), precipitation ( $-21.9 \pm 3.6\text{‰}$ ) and soil water under dead grasses ( $-35\text{‰}$ ) – see Figure 7b, d. This  $\sim 11\text{‰}$   $\delta\text{D}$  depletion could be explained by (i) a fractionation process in the soil during water redistribution at night by tree root tissues. During this redistribution a chain of phase transitions from liquid to vapour takes place. While the lighter water vapour molecules diffuse faster through the soil pore volumes, away from the rhizosphere, the remaining water becomes enriched through kinetic fractionation. Meanwhile the tree tissue is replenished with

the more enriched ground water. This leads to an enriched xylem water isotope signal, relative to the soil water, which is now in further distance from the rhizosphere. There the depleted water condenses as the pore volumes get saturated and the soil temperature decreases, accumulating the lighter water over night. As the soil temperature will rise during the day this accumulated and depleted bulk soil water will evaporate again undergoing another fractionation. Part of this water (predominantly depleted, as a result of the kinetic fractionation) will evaporate to the atmosphere while a back diffusion towards the rhizosphere takes place, since the roots utilized the water closest to the rhizosphere, creating an inverse water vapour gradient in the soil compared to the previous night. Thus the remaining predominantly depleted water will diffuse back to the roots where it is utilized by plants.

Figure 7 shows different isotopic patterns between  $\delta^{18}\text{O}$  and  $\delta\text{D}$  in the soil water profile. The isotopic effects for deuterized water is more expressed because the deuterium atom is twice as heavy as hydrogen leading to much lower vibration frequencies and thus to significantly higher molecular bond strength than for the  $\text{H}_2^{18}\text{O}$  molecule, where the  $^{18}\text{O}$  atom is only 12.5% heavier than the  $^{16}\text{O}$  atom. Consequently the isotopic effect is smaller for  $\text{H}_2^{18}\text{O}$  than for DHO water (Barrow, 1962; Lin and Sternberg, 1993). Furthermore, DHO would accumulate close to the fine root zone, while a higher diffusion rate of lighter, depleted water into the bulk soil zone occurs. This fractionation process takes place along with HL during the night, due to water release by the roots. This explains the large range in  $\delta\text{D}$  values observed in xylem water in September among the 27 measured trees ( $-33$  to  $-44\text{‰}$ ), and may be a good index for the ability of each tree to perform HL and to have access to deep groundwater sources.

It is note worthy that (ii) a fractionation process due to water uptake by the roots was observed by Lin and Sternberg (1993). The authors concluded that a 3–11‰ deuterium discrimination was occurring in roots during water uptake. However, they were the only authors demonstrating a hydrogen fractionation at the root level and only in halophytic plants. So far all the other published studies using stable

isotope analysis for water source determination under arid or Mediterranean climates did not find any deuterium fractionation during water uptake by roots (Boutton et al., 1999; Donovan and Ehleringer, 1994; Midwood et al., 1998). Therefore we may exclude any fractionation during water uptake by roots in this study as well.

*Impact of hydraulic lift on tree water status and contribution to the local water balance*

Significant linear negative relations between isotopic signature in tree xylem sap and  $\Psi_L$  measured at different times of the day and at night were found in September (Figure 8, Table 1). Trees with better water status presented a more negative  $\delta D$  and  $\delta^{18}O$  isotopic ratios of xylem sap. Moreover, the trees for which HL was substantiated by diel  $\Psi_s$  fluctuations (A13, D6, D22) showed intermediate isotopic signature and water status. These results strongly suggest that depleted isotope signatures in xylem sap may be linked to HL, and also that the process may have a significant positive impact on tree water status at the peak of the drought. Jackson et al. (1995) and Filella and Peñuelas (2003) also found a significant negative relationship between xylem isotopic composition and  $\Psi_L$ . Since depletion of heavier isotopes in soil water increased with depth, they concluded that plants with better water status obtained water from deeper soil layers. Similar conclusions were proposed by Otieno et al. (in press) and are supported by other studies that showed higher water stress in shallow-rooted compared to co-occurring deep-rooted species (Flanagan et al., 1992; Thornburn et al., 1994; Valentini et al., 1992).

Emerman and Dawson (1996) estimated that *Acer saccharum* lifted  $102 \pm 54$  L of water each night. Using the same model, Ludwig et al. (2003) estimated that the volume of water lifted by *Acacia tortilis* could reach 70–235 L for an average diel  $\Psi_s$  fluctuation of  $-0.15$  MPa. In our study, we showed that the nocturnal increase in  $\Psi_s$  obtained under each tree was due to HL, while the diurnal decrease corresponded to the average tree daily transpiration (Figure 3). According to the amplitude of the decrease and the increase of the  $\Psi_s$  curves in Figures 3 and 4,

we roughly estimated that the hydraulically lifted water accounted for 50–100% of the following day's transpiration, from July to August. Knowing that the mean daily transpiration flux of the trees varied between 0.5 L and 17.6 L day<sup>-1</sup> during the same period (Table 1), we estimated that 0.25–8.8 L of water were daily redistributed into the *Q. suber* rhizosphere from July to September. This amount of water is much lower compared to the values estimated by Ludwig et al. (2003) for *Acacia tortilis* trees (70–235 L day<sup>-1</sup>). This difference can be explained by the small diameter ( $0.12 \pm 0.06$  m) and crown-projected area ( $5.0 \pm 0.3$  m<sup>2</sup>) of the trees in our experimental area, compared to the trees measured by Ludwig et al. (2003), which were approximately 100-years old and had an average DBH of 59 cm.

According to Dawson (1993b), the contribution of each source to tree transpiration can be estimated according to the following end-members partitioning equation:

$$\delta D_{\text{xylem}} = A\delta D_{\text{source1}} + (1 - A)\delta D_{\text{source2}} \quad (2)$$

with A representing the proportion of water.

Considering that  $\delta D_{\text{xylem}}$  varied among trees between  $-33$  and  $-44\%$  in early September, and solving the equation using these two values successively, we estimated that a direct use of groundwater from the aquifer ( $\delta D_{\text{source1}} = -29.8\%$ ) contributed for 19–83% of water transpired by *Q. suber* trees. Therefore 17–81% (corresponding to 0.1–14 L tree<sup>-1</sup> day<sup>-1</sup>) of deep water lifted into the rhizosphere by HL ( $\delta D_{\text{source2}} = -47.0\%$ ) contributed to tree transpiration at the peak of the drought period, with larger contributions from trees presenting the lowest  $\delta D_{\text{xylem}}$  values (Figure 8). Measuring soil water storage and root sap flux in a 20-year old Douglas-fir stand, Brooks et al. (2002) found that HL contributed to about 28% of the total daily water use from the upper 2 m of the soil profile during the drought period. However, our quantitative estimates of the contribution of HL to the local water balance using stable isotope data should be considered with caution, due to the lack of replication in soil profile samples, and since further studies in such habitats need to confirm our conclusions.

Nevertheless, our results emphasize the importance of deep rooting and HL as

adaptation mechanisms to Mediterranean summer drought in *Q. suber*, improving plant water status (David et al., 2004; Walter, 1973). The advantages of deep rooting and HL for avoiding or reducing water stress have also been reported for many other species under dry conditions (Grieu et al., 2001; Horton and Hart, 1998; Klepper, 2001; Peñuelas and Filella, 2003; Ryel et al., 2002). This phenomenon may be most effective in Mediterranean environments with precipitation concentrated in winter when the low potential evapotranspiration allows a surplus of water to infiltrate for later use by deep rooted plants (Sankaran et al., 2004).

Lifted water may also partly re-wet the upper soil layers allowing some microbial activity and organic matter mineralization while keeping fine roots alive and able to absorb nutrients. This may be especially important during the burst in soil heterotrophic respiration that occurs with the onset of autumn rains. At this time of the year, herbaceous plant roots are not alive in the top soil to use the suddenly available nutrients and rain water is not plentiful enough yet to carry them deep into the soil (Pereira et al., 2004). With HL, trees may benefit from nutrients even when the amount of rainfall is too small to have any effect on plant water status, if they have viable roots below the 0.3–0.4 m horizon (Canadell and Zedler, 1995).

## Conclusions

Using stable isotopes and equitensiometers, we showed that in *Q. suber*, roots located between 0.4 and 1 m depth were responsible for water uptake during the day whereas another set of roots reaching deeper subsoil layers or the groundwater were responsible for water transport during the night via HL. In a savannah-type Mediterranean system, new root formation in deeper soil layers accompanying the interruption of shoot growth in the dry summer and hydraulic lift are significant adaptation traits to counteract negative drought stress effects, improving access to deeper available water and/or reducing tree transpiration. The large amount of water calculated to be redistributed may represent an appreciable fraction of daily transpiration and was shown to substantially improve plant water status. Hydraulic

lifted water may also enhance or maintain fine-root activity by keeping them hydrated, thus permitting efficient nutrient uptake in a climate with marked rainfall seasonality.

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