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Water relations of cork-oak (*Quercus suber* L.) under natural conditions

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Abstract

Daily and annual courses of leaf transpiration, stomatal conductance and shoot water potential of four *Quercus suber* individuals were compared in a semi-natural stand in southwest Portugal, from spring 1989 to early summer 1990.

The trees investigated showed annual patterns typical of evergreen sclerophyllous species but varied in their range of stomatal operation. This appeared to be related to differences in hydraulic conductivity in the root-to-leaf pathway.

Maximum stomatal conductance and transpiration rates occurred from March to June.

Water stress was found to be moderate and winter cold stress due to low air and soil temperatures appeared to have an influence on plant water balance through their effects on flow resistances.

Abbreviations: g_{sw}, stomatal conductance; g_{max}, maximum stomatal conductance, PAR, photosynthetically active radiation; RH, relative humidity of the air; T, leaf transpiration; Ta, air temperature; TL, leaf temperature; T_{max}, maximum leaf transpiration; ΔW, air-to-leaf vapor pressure difference; Ψ, shoot water potential; ΨPD, predawn shoot water potential; ΨMIN, minimum shoot water potential.

Introduction

Human activity has been responsible for the development of several managed ecosystems which are still found over a large area of the Iberian Peninsula. Such systems, called *dehesa* in Spain and *montado* in Portugal, are dominated by the evergreen oaks, *Quercus ilex* and *Quercus suber*. These oaks occur in pure or in mixed stands, and hybridization is frequent (Vasconcellos & Franco 1954).

In Portugal, the *montado* is an important component of the landscape, occupying vast areas on schistic and granitic soils, south of the river Tejo. Cork-oak stands are mainly found in the Atlantic-influenced western areas, while holm-oak is more abundant in the eastern drier regions.

Quercus suber, the primary source of industrial cork, is one of the most important woody species occurring in Portugal. It is drought resistant and it can grow on very poor soils, due to its structural and physiological xerophytic adaptations.

It is known that cork-oak populations have been decreasing in mediterranean areas mainly due to improper land and crop management (Natividade 1957). In Portugal they are still widespread, although aging and debilitation have become apparent in some areas.

The evergreen habit of many mediterranean species, especially of those species which do not reduce their transpiring biomass, seems to be in disharmony with the bi-seasonal mediterranean climate involving summer drought stress and winter cold stress (Mitrakos 1980; Orshan 1986).

Plant production under mediterranean climates is, in general, limited by cold temperatures and low irradiance during the winter months and high temperatures combined with increasing water stress as the summer drought progresses. The way in which individual species react to these stresses has been the object of several studies (Kummerow *et al.* 1981; Monney 1981; Harley *et al.* 1987; Correia 1988).

Like many evergreen sclerophyllous species that are sensitive to winter cold stress (Mitrakos 1980), *Q. suber* may be affected by winter temperatures since it commences growth only after May. The deep root system probably contributes to this by keeping the water potential at a high level even during the summer period.

Data regarding ecophysiological responses of *Q. suber* under natural conditions are rather scarce, although recent studies have been done on the ecophysiology of some sclerophylls growing in natural Portuguese maquis, in particular on *Q. coccifera* (Tenhunen *et al.* 1985; 1987) and *Q. suber* (Tenhunen *et al.* 1984; 1987).

In the present study an investigation of the water relations of *Quercus suber* under natural conditions has been conducted. This work is part of a project developed to examine the factors affecting primary production of this species throughout annual cycles, particularly during periods of stress when rates of productivity sharply decrease. Moreover, the results may provide an important basis for assessing the function and dynamics of the important mediterranean ecosystems such as *Q. ilex* and *Q. suber dehesas* and *montados*.

Materials and methods

Site description

This study took place in a semi-natural cork-oak stand approximately 10 km north of Santiago do Cacém (38 05′ N, 8 39′ W, elevation 290 m), in southwest Portugal. A sandy silt-loam soil is established on a Carbonic turbiditic bedrock. The annual rainfall averages 760 mm and the mean annual temperature is 15.5 °C, with a mean minimum temperature for the coldest month of 6.0 °C (values from 1941–70). Rainfall and air temperatures during the study period are shown in Figure 3a.

The stand is a typical *montado*, with a tree layer of dispersed *Q. suber* individuals (*ca.* 93 trees/ha) exploited for cork production, and a herbaceous layer used for pasture.

Methods

This work was carried out from spring 1989 to early summer 1990. Diurnal courses of Ψ, T and g_{sw} rates and environmental factors were recorded from dawn to sunset once a month during this period. In the present paper, daily courses are shown for three months, considered representative of the different seasons.

Simultaneous measurements of shoot water potential, Ψ, (with a Scholander-type pressure bomb), leaf transpiration, T, and conductance, g_{sw} (with a steady-state porometer LI-COR LI-1600) were performed. For each tree data

Table 1. Some characteristics of the trees under study. DBH (diameter at breast height), H (height), C (mean crown diameter) and D (mean trunk-to-trunk distance to the nearest trees).

Tree	DBH (m)	H (m)	C (m)	D (m)
1	0.46	7.8	11.4	11.7
2	0.40	12.6	16.9	9.9
3	0.38	8.2	8.9	8.6
4	0.50	9.7	14.5	6.9

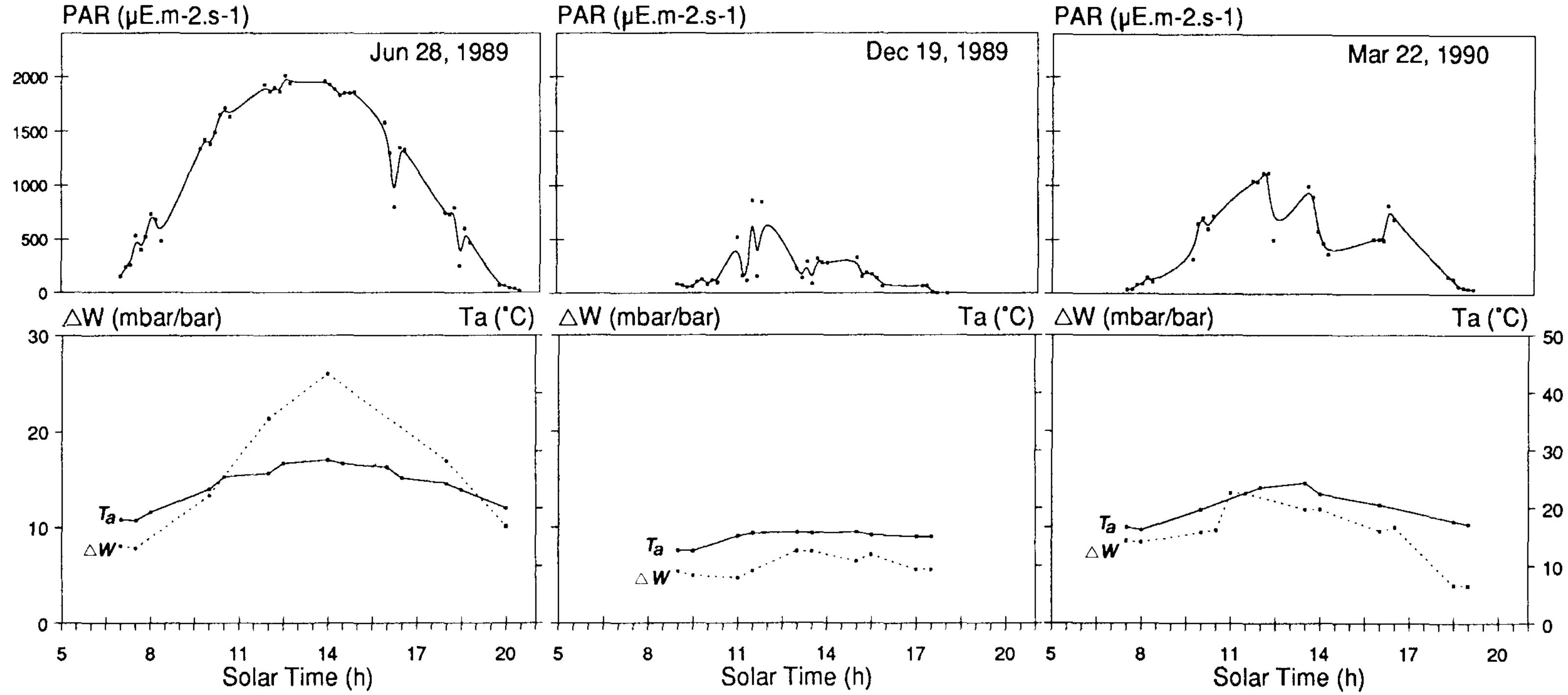


Fig. 1. Diurnal variation in climatic conditions for three different days at the study site-photosynthetically active radiation (PAR), air-to-leaf vapor pressure difference (ΔW) and air temperature (Ta) (Santiago do Cacém, Portugal).

points given are the mean of the measurements made on three terminal branches and leaves. For T and g_{sw} the same leaves were measured throughout the day. All the samples were taken from the south side of the canopy, at a 1.5–2 m height. g_{sw} was calculated on a leaf area basis from T and ΔW (air-to-leaf vapor pressure difference).

Soil-to-leaf hydraulic conductivity was calculated as the absolute value of the slope of linear regressions between T and Ψ (Elfving *et al.* 1972; Kaufmann 1979; Küppers *et al.* 1987; Reich & Hinckley 1989). The morning water potential used at $T = 0$ was the ΨPD.

The data refer to four trees (numbered 1 to 4). These trees were chosen for their phenotypical similarity (height, canopy structure, breast height diameter) and proximity (all within a 4500 m^2 area). In Table 1 some of their characteristics are shown. Care was taken in choosing individuals stripped of their bark in the same year (1988), since the process is known to affect the physiology of cork-oak trees (Natividade 1950).

Results and discussion

Diurnal patterns

Diurnal patterns of environmental conditions, leaf transpiration, total leaf conductance and shoot water potential are shown for 3 days: June 28 (1989), December 19 (1989) and March 22 (1990) (Figs. 1 and 2).

In general, dome-shaped diurnal patterns were found for T and g_{sw}. Maximum T rates occurred around midday (Fig. 2). The exception presented by tree 2 is probably due to partial shading by nearby trees in the early afternoon. This tree shows higher values of T and g_{sw} in the morning which steadily decrease afterwards, associated with the recovery of water potential.

On December 19 and March 22 low levels of PAR resulted from cloudy weather (Fig. 1). In winter (December 19) PAR remained below 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ and Ta ranged between 12 and 15 °C; hence T and g_{sw} were very low for the trees studied, with no marked differences between them. On March 22 a decrease in T and g_{sw} was observed in early afternoon due to a sudden decrease in PAR from 1000 to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. 1 and 2c).

Differences between trees were clearer in June 28 and March 22, when more favorable environmental conditions occurred.

Midday stomatal closure, already shown for *Quercus suber* and other sclerophylls (Tenhunen *et al.* 1981; 1984; 1987; Lösch *et al.* 1982; Lange *et al.* 1982), was not observed during this study neither in the presented data nor on hot days in July and August (unpublished data). It is possible that summer drought stress at our study site was not strong enough to produce such effects on the trees. Nevertheless, the absence of midday stomatal closure has also been described for *Quercus* species by other authors (Sala Serra *et al.* 1990; Acherar *et al.* 1991).

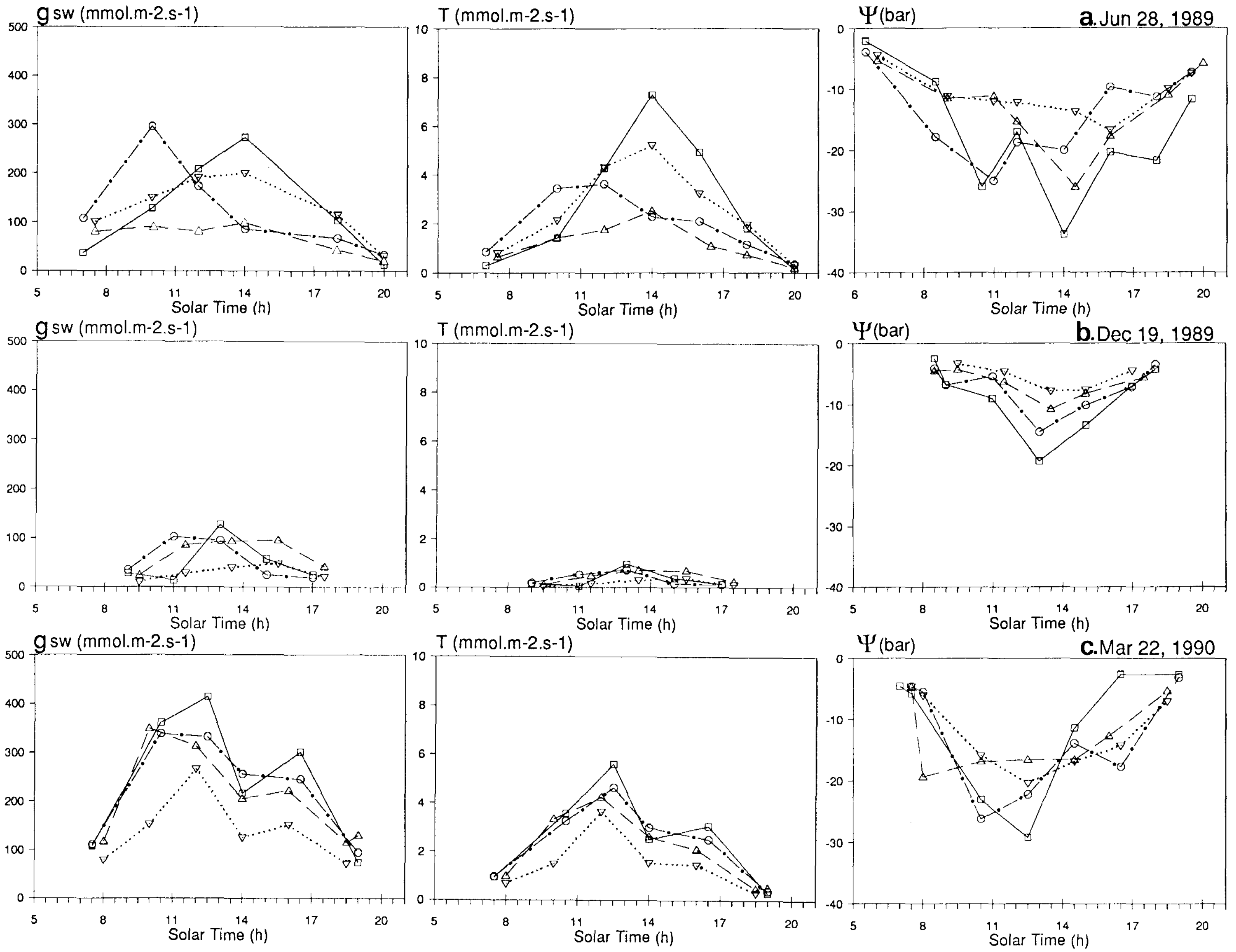
Shoot water potential generally reflected leaf transpiration rate, with the lowest potential (ΨMIN) occurring at the highest T rates (Fig. 2).

Annual patterns

The study trees displayed annual patterns of ΨMIN and g_{max} typical of most evergreen sclerophyllous species and similar to those reported for other mediterranean oaks, *Q. coccifera* and *Q. suber*, by Tenhunen *et al.* (1987) (Fig. 3b).

Throughout the year ΨPD was relatively con-

Fig. 2. Diurnal courses of stomatal conductance (g_{sw}), leaf transpiration (T) and shoot water potential (Ψ) on three different days, for the four *Q. suber* trees under study – tree 1 (-⊟-), 2 (-⊖-), 3 (-▽--) and 4 (··△··) (Santiago do Cacém, Portugal).
a. June 28, 1989
b. December 19, 1989
c. March 22, 1990.


gsw (mmol.m-2.s-1)
T (mmol.m-2.s-1)
Ψ(bar)
a.Jun 28, 1989
b.Dec 19, 1989
c.Mar 22, 1990
Solar Time (h)
500
400
300
200
100
0
10
8
6
4
2
0
-10
-20
-30
-40
5
6
8
11
14
17
20

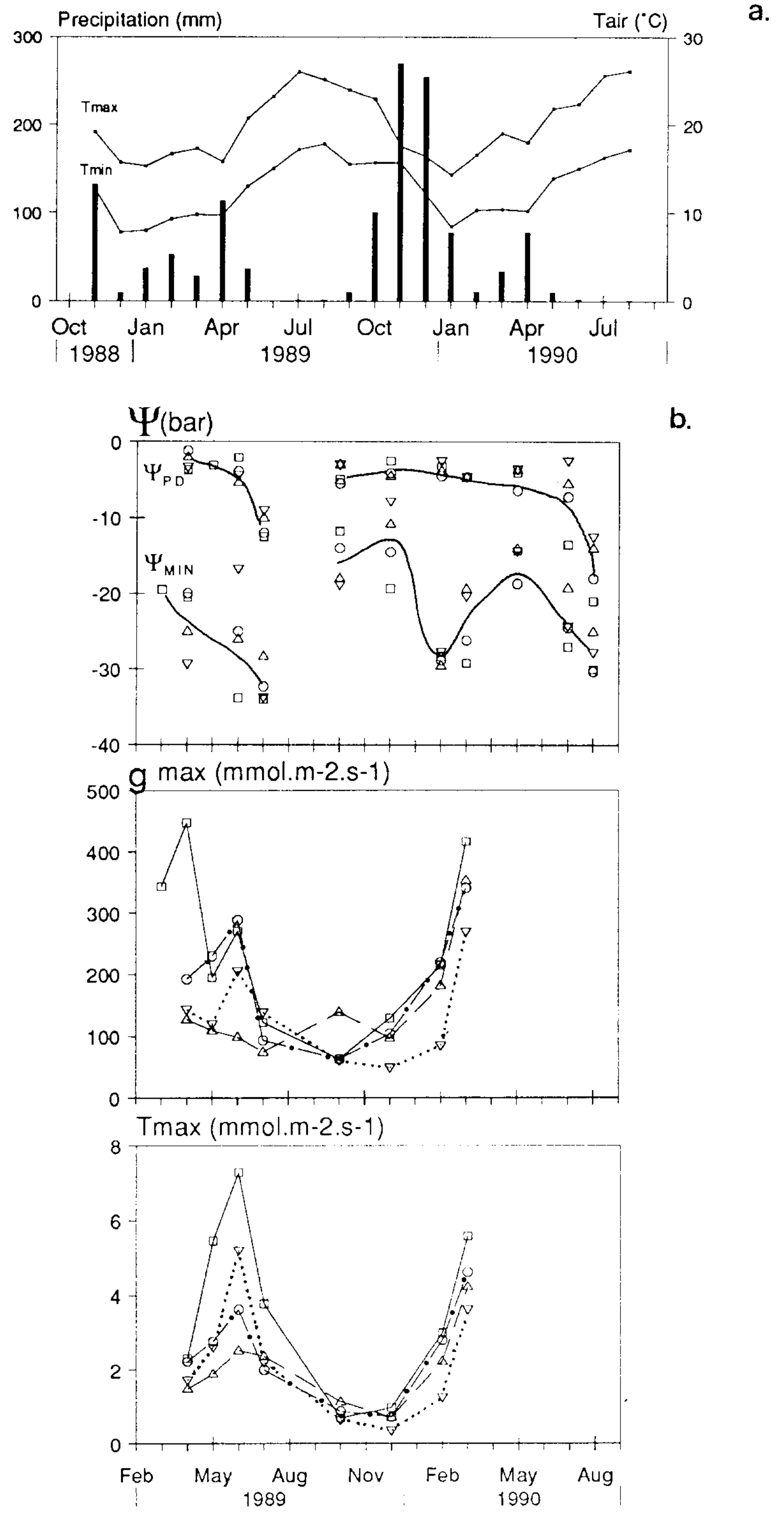


Fig. 3. (a) Monthly rainfall and mean air temperature recorded at a nearby station, from autumn 1988 to summer 1990; (b) Seasonal trends of predawn and minimum shoot water potential (ΨPD and ΨMIN), maximum conductance (g_{max}) measured on the four *Q. suber* trees under study. For Ψ, only the mean courses are drawn. Tree 1 (-⊟-), 2 (-⊖-), 3 (-▽-) and 4 (··△··) (Santiago do Cacém, Portugal).

stant during the wet season (*ca.* −3 bar, Fig. 3), ranging from −1.5 bar in April 1989 to −21 bar in August 1990. These values are similar to those reported by Poole & Miller (1975), Tenhunen *et al.* (1987), Harley *et al.* (1987) and Correia (1988) in species with deep and extensive root systems, suggesting high water availability for all trees during the year. Only during the driest months (July and August 1990) were different ΨPD values observed, trees 1 and 2 apparently being more affected by water shortage than trees 3 and 4: −14, −7 bar *vs.* −3, −6 bar in July; −21, −18 *vs.* −13, −14 bar in August (Fig. 3b). It is possible that proximity to neighboring trees (Table 1) played an important role in the maintenance of higher water availability at the root level for trees 3 and 4, as has been suggested by Joffre & Rambal (1988), but different root depths may have also contributed to our observations.

The ΨMIN, generally occurring around midday, ranged from −8 bar in the wet season (December 1989) to −34 bar in July 1989 (Fig. 3). The low values ΨMIN measured in February and March 1990 are probably related to high T rates developed under unusually favorable weather conditions.

Leaf conductance varied seasonally (Fig. 3b), being lowest in winter and summer; the higher values in spring are associated with high soil moisture and moderate temperatures. Maximum stomatal conductance was observed in June 1989 (100–290 mmol·m^{-2}·s^{-1}) and in March 1990 (270–420 mmol·m^{-2}·s^{-1}) with similar values to those reported by Tenhunen *et al.* (1987) for *Q. suber*. T_{max} exhibits the same pattern with maximum values of 2.5–7.2 mmol·m^{-2}·s^{-1} in June 1989 and 3.6–5.6 mmol·m^{-2}·s^{-1} in March 1990.

Hydraulic conductivity

Fluctuations around the general pattern of ΨMIN annual course (Fig. 3), which are not apparent for ΨPD annual course, may be explained by differences in the hydraulic conductivity system of the trees, as suggested by the T/Ψ relationship (Table 2) using the model of soil-plant-atmosphere continuum (Elfving *et al.* 1972).

In fact our data showed a linear relationship between shoot water potential and transpiration rate for these trees (Fig. 4). This observation is consistent with many other investigations (Hinckle & Bruckerhoff 1975; Kaufmann 1979; Küppers 1984; Küppers *et al.* 1987; Reich & Hinckley 1989). Such results suggest that the internal plant resistance remains constant with changing rates of flow as assumed in the flow model of Elving *et al.* (1972). The soil-to-plant conductivity remained constant within a T range of 0–7.3 mmol·m^{-2}·s^{-1} in June 28 (1989) and of 0–1.0 mmol·m^{-2}·s^{-1} in December 19 (1989).

However this conductivity was not constant over the year, as shown by the slopes of the regressions in Figure 4, and differed among trees (Table 2). This variability between individuals may be due to a non-uniform root distribution and different canopy development which is known to play an important role in hydraulic conductivity (Küppers 1984).

The hydraulic resistance ranged from 1.6 bar·mmol^{-1}·m^{2}·s in June 28 (1989) to 15.4 bar·mmol^{-1}·m^{2}·s in December 19 (1989), with intermediate values on March 22 (1990) (Table 2). The different regression lines have similar origin values (at T = 0), *i.e.*, the maximum water poten-

Table 2. Relationship between leaf transpqiration (T) and shoot water potential (Ψ). Linear regressions used for the estimation of the hydraulic resistance are shown.

Date	Tree	Linear regression	n	R^2	Signif. level
June 28, 1989	1	$\Psi = -7.9 - 3.3\ T$	7	0.82	*
	2	$\Psi = -5.4 - 4.3\ T$	7	0.88	**
	3	$\Psi = -6.9 - 1.6\ T$	7	0.78	*
	4	$\Psi = -5.1 - 6.9\ T$	8	0.92	**
December 19, 1989	1	$\Psi = -5.3 - 15.4\ T$	6	0.87	**
	2	$\Psi = -5.6 - 8.4\ T$	6	0.39	–
	3	$\Psi = -2.9 - 14.0\ T$	5	0.95	**
	4	$\Psi = -3.8 - 7.6\ T$	6	0.84	*
March 22, 1990	1	$\Psi = -7.6 - 2.8\ T$	5	0.28	–
	2	$\Psi = -2.3 - 5.2\ T$	7	0.85	**
	3	$\Psi = -7.9 - 2.1\ T$	7	0.28	–
	4	$\Psi = -8.0 - 2.6\ T$	7	0.47	–

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

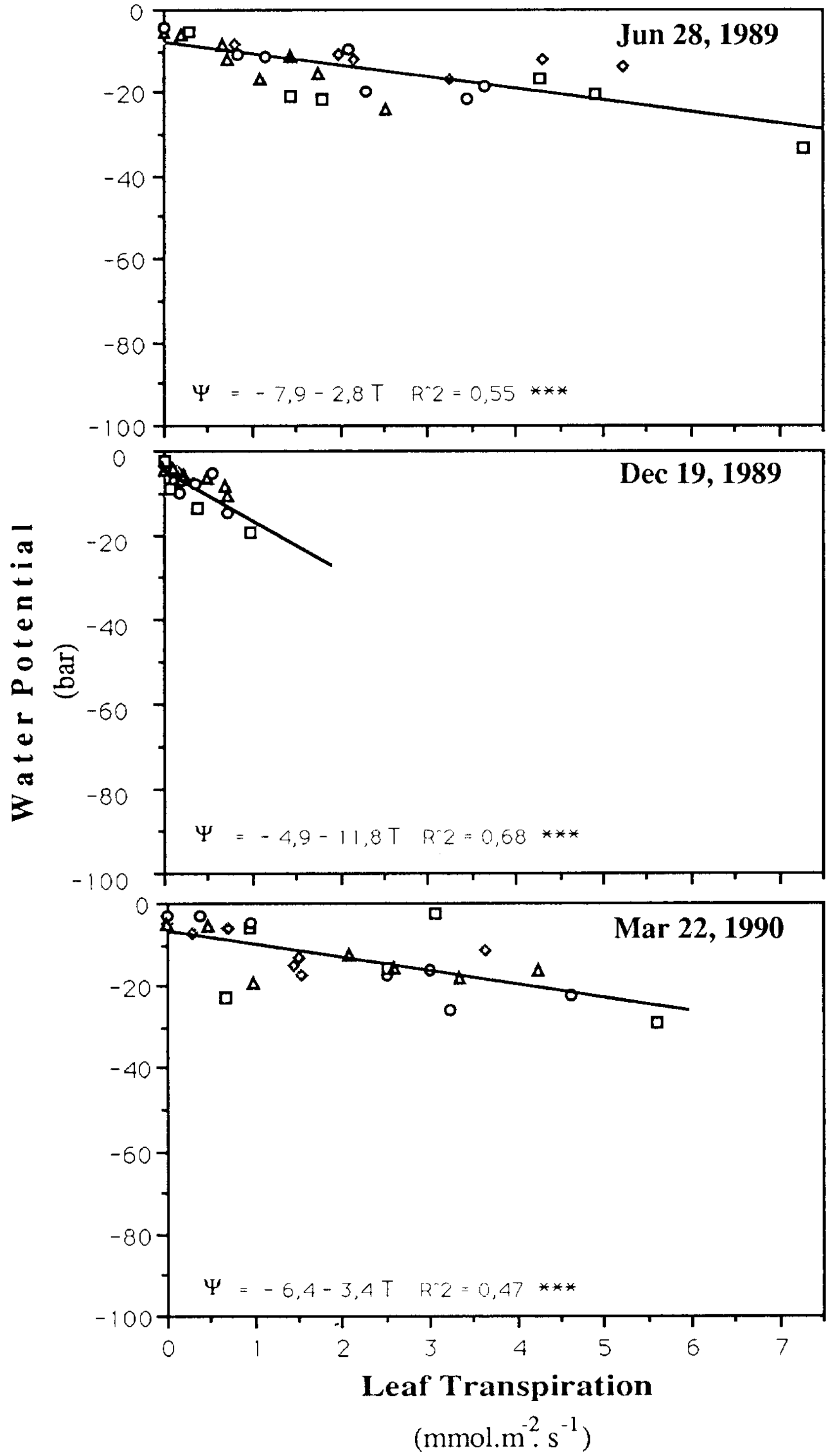


Fig. 4. Relationship between leaf transpiration rate (T) and shoot water potential (Ψ) taken from the diurnal courses (Fig. 2). The linear regression shown for each month refers to the four trees all together. Regressions were all significant ($p < 0.001$). Tree 1 (□), 2 (○), 3 (◇) and 4 (△) (Santiago do Cacém, Portugal).

tial reached during the night on these three dates was relatively constant ($\Psi_{PD} \approx -3$ bar). Thus a limiting water flow conductance, rather than seasonal variations of soil water availability, seems to be the reason for different hydraulic resistances.

The liquid phase conductance seems to be temperature dependent. In June, with higher temperatures and water availability, the hydraulic conductivity is higher (Fig. 3 and Table 2) indicating an adequate transport of water during this period, which was coincident with the period of vegetative growth (Oliveira *et al.* 1991). On warmer days (March 22 and June 28) the slopes did not differ greatly (Fig. 4), while in December lower Ψ occurred at similar T fluxes.

Tenhunen *et al.* (1989) also reported little change in the hydraulic resistance from May to September for *Q. coccifera*, in spite of a substantial decrease of water availability during this period. It was not possible to confirm a similar result with the present work, due to insufficient data from the driest months (August and September). However, the available values from July 1989 (not shown) seem to indicate that when Ψ_{PD} values are lower than the annual average, the hydraulic resistance is much higher than during the previous spring.

This study suggests that root and/or leaf temperatures during winter may play an important role for this species, similar to that found for *Q. ilex* (Comín *et al.* 1987; Sala *et al.* 1989). In December, in spite of the higher Ψ, the hydraulic resistance was very high, probably due to a decrease in either the efficiency of water uptake by the roots or of the root-to-leaf pathway conductivity. Such an increase in hydraulic resistance was also found in *Q. coccifera* only during cold winter periods (Tenhunen *et al.* 1989).

Final remarks

This work demonstrates differences in the ability of *Q. suber* trees growing in the same stand to exploit water resources. The investigated trees varied in their range of stomatal operation. This appeared to be related to hydraulic conductivity differences in the root-to-leaf pathway. Such an intra-specific variability in terms of water relations has also been reported by other authors for several mediterranean oaks, including *Q. suber* (Acherar *et al.* 1991).

The water stress was moderate at our study site and winter cold stress was probably more important. Lower air and soil temperatures which are likely to occur in winter apparently influenced plant water balance through their effects on flow resistances (Fig. 3 and Table 2).

The variability in the water transport efficiency may be related to different phenotypes resulting from interspecific hybridization, which is known to occur frequently (Vasconcellos & Franco 1954). Seasonal changes in the canopy architecture and root system might also play an important role in these variations. Further work is needed to test these hypotheses.

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