Metadata of the chapter that will be visualized online

Series Title	Ecological Studies	
Chapter Title	How Mediterranean Deciduous Trees Cope with Long Summer Drought? The Case of <i>Quercus pyrenaica</i> Forests in Western Spain	
Chapter SubTitle		
Copyright Year	2011	
Copyright Holder	Springer Science + Business Media B.V.	
Corresponding Author	Family Name	Moreno
	Particle	
	Given Name	Gerardo
	Suffix	
	Division	Forestry School
	Organization	University of Extremadura
	Address	10600, Plasencia, Spain
	Email	gmoreno@unex.es
Author	Family Name	Gallardo
	Particle	
	Given Name	Juan F.
	Suffix	
	Division	
	Organization	CSIC, I.R.N.A.
	Address	37071, Salamanca, Spain
	Email	
Author	Family Name	Vicente
	Particle	
	Given Name	María Ángeles
	Suffix	
	Division	
	Organization	CSIC, I.R.N.A.
	Address	37071, Salamanca, Spain
	Email	
Abstract	<p>The functional characteristics of Mediterranean deciduous trees provide an interesting model for investigating adaptative mechanisms to drought, useful to understand future changes of northern forests in scenery of climate change. In this article we analyse how a Mediterranean deciduous oak, <i>Quercus pyrenaica</i>, with a short vegetative period coincident with summer drought, cope with water deficit in that period. We revised published data on temporal dynamic of soil moisture and physiological status of tree leaves of several forest stands of Central–Western Spain and discuss the significance of soil water reserve and deep rooting system on the maintenance of tree transpiration and physiological activity of the trees along summer drought. Results revealed that (i) <i>Q. pyrenaica</i> oak is only slightly water-limited during summer drought, (ii) <i>Q. pyrenaica</i> oaks depend on thick weathered, porous bedrocks, and (iii) <i>Q. pyrenaica</i> is a well-performing deciduous oak to cope with increasing summer drought.</p>	
Keywords (separated by '-')	Soil water dynamic - Leaf water potential - Stomatal conductance - Evapotranspiration - Adaptative traits - Rainfall gradient	

Chapter 10 1
How Mediterranean Deciduous Trees Cope 2
with Long Summer Drought? The Case 3
of *Quercus pyrenaica* Forests in Western Spain 4

Gerardo Moreno, Juan F. Gallardo, and María Ángeles Vicente 5

Keywords Soil water dynamic • Leaf water potential • Stomatal conductance 6
• Evapotranspiration • Adaptative traits • Rainfall gradient 7

Introduction 8

Most of the climate change models predict an increase of aridity of the Mediterranean 9
basin and that drought episodes could be more frequent in the present century due to 10
climate change (IPCC 2007). Similar changes are also expected in temperate regions 11
in the Northern Europe (Bréda et al. 2006) and South-Eastern Europe (Chapter 8, 12
this volume), with direct consequences on forest health. A massive dieback of oaks 13
forest (both evergreen and deciduous) has been observed some summers in last 14
decades (Peñuelas et al. 2001; Corcuera et al. 2004), and several authors have 15
shown how some mesic Mediterranean trees could be replaced for other more xeric 16
species under the current scenario of climate change in Mediterranean forests 17
(Martínez-Vilalta et al. 2002; Peñuelas and Boada 2003). 18

The functional characteristics of Mediterranean deciduous trees provide an 19
interesting model for investigating adaptative mechanisms to drought, useful to 20
understand future changes of northern forests in a scenario of climate change 21
(Baldocchi and Liukang 2007). The genus *Quercus* comprises 531 tree and shrub 22
species distributed among contrasting phytoclimates in the Northern Hemisphere, 23
from temperate and subtropical deciduous forests to dry Mediterranean evergreen 24
woodlands (Corcuera et al. 2002). The range of variation in the ecophysiology of 25
Mediterranean oaks is comparable to that observed between other deciduous and 26

G. Moreno(✉)
Forestry School, University of Extremadura, Plasencia 10600, Spain
e-mail: gmoreno@unex.es

J.F. Gallardo and M.Á. Vicente
CSIC, I.R.N.A., Salamanca 37071, Spain

evergreen species in the Mediterranean basin (Duhme and Hinckley 1992), in the Californian chaparral (Blake-Jacobson ME 1987) and in Tropical dry forests Sobrado (1986). Corcuera et al. (2002) identified three phytoclimatic groups of *Quercus*, which were characterized by their contrasting ecophysiological response to water stress. They found that Mediterranean deciduous oaks perform better than temperate deciduous oaks under water-stress conditions, the last having difficulties to thrive in dry soils. Valladares et al. (2004) predicted that Mediterranean deciduous oaks will be replaced by evergreens, and the former species will extend in areas currently occupied by temperate deciduous oaks.

The main characteristics defining Mediterranean ecosystems generally are the scarcity and irregularity of rainfall (P) and potential evapotranspiration (E_p) values, the latter usually higher than the former in an annual basis. Mountainous areas, where Mediterranean deciduous oaks are mostly located, exhibit similar or higher P than E_p values, but a much higher evaporative demand than rainfall during summer, in addition to long and cold winters. These climate conditions determine that deciduous oaks have a short growing season (around 120 days year⁻¹), mostly coincident with the period without rain. Deciduous leaves can be as costly to produce as evergreen leaves (Merino et al. 1982) and in a relatively short time, should maintain a high photosynthetic activity throughout summer to obtain a positive annual C balance. This pattern clearly contrasts with that of Mediterranean evergreen species, which are photosynthetically active all year. Evergreen oaks gain significant amounts of C in winter period, and water stress usually cause stomatal closure early in the growing season (Rodá et al. 1999).

Under these circumstances, Mediterranean deciduous trees surely exhibit a high dependence on soil water reserves (SWR) accumulated on soil along wet season. This reserve however could be limited in many sites because of the frequent shallowness of Mediterranean soils. The investment on very deep root systems is a morphological traits frequently associated to Mediterranean evergreen species (Canadell et al. 1996; Moreno et al. 2005). However this trait was scarcely studied in Mediterranean deciduous trees yet. We hypothesised that Mediterranean deciduous oaks have also very deep root systems and use bedrock water reserve; this powerful root system entails a resource use allowing an increment in the aboveground production.

Apart of the use of SWR, Mediterranean deciduous forest could exhibit a set of anatomical and physiological traits compatible with long summer drought. In this article we also analyse the diurnal and seasonal dynamic of stomata conductance on one hand and, on the other hand, a set of potential of morphological/physiological traits that could contribute to increasing the water use efficiency (WUE).

Stomata regulation is considered the most immediate mechanism of the optimisation of C-gain/water-loss in plants (Rambal 1993) and we hypothesised that deciduous trees exhibit a non-conservative pattern of water transpiration (stomata activity), contrary to their neighbour or co-existing evergreen trees (Damesin et al. 1998). The reduction of leaf area index (LAI) is a third mechanism associated to optimisation of WUE and, presumably, Mediterranean deciduous oaks have low LAI compared to congeneric species, either temperate deciduous or Mediterranean evergreen oaks.

Given the wealth of information that exists on water dynamics of temperate coniferous and deciduous broadleaves (e.g., Bréda et al. 2006), and Mediterranean evergreen trees and forests (e.g., Rodá et al. 1999; Ciais et al. 2003), corresponding knowledge is scarce about Mediterranean deciduous species. The understanding of these southern deciduous forests is needed for modelling water budgets and water yield, planning forest conservation and/or restoration programmes, and understanding the future dynamic of both Mediterranean and temperate forests under current scenarios of climate change.

In this article we analyse how a Mediterranean deciduous oak, *Quercus pyrenaica*, with a short vegetative period coincident with summer drought, cope with water deficit in that period. We revised published data on temporal dynamic of soil moisture and physiological status of tree leaves of several forest stands of Central–Western Spain and discuss the significance of soil water reserve (SWR) and deep rooting system on the maintenance of tree transpiration and physiological activity of the trees along summer drought. Accordingly, the following three questions are addressed: (a) Are trees water-limited during summer drought? (b) What is the tree water source during summer drought? and (c) Which adaptative mechanisms exhibit this species to face water deficit?

Study Species

Quercus pyrenaica is a slow-growing Mediterranean deciduous species, distributed throughout mountainous sub-humid Mediterranean areas of the southwestern region of Europe, especially in the western regions of the Iberian Peninsula. It has a short growing season (from the end of May till mid October), which may determine its distribution. The species is well adapted to survive maintaining photosynthetic production in spite of the long summer water deficit (Gallego et al. 1994; Rico et al. 1996) and, therefore, it often occupies transitional areas from sub-humid to semi-arid conditions (Hernández-Santana et al. 2008a). Despite its distribution and interesting ecology, *Q. pyrenaica* has been poorly studied in comparison with other Mediterranean *Quercus* species (Silla and Escudero 2006), probably because of its low aboveground productivity (Gallardo 2000).

A common strategy to thrive on water-limited conditions is the reduction of the transpiration area (Rambal 1993); then, leaf area index (LAI) usually decreases with water deficit (Grier and Running 1977; Ogaya and Peñuelas 2007). Hernández-Santana et al. (2008a) have reported an average value of $2.4 \text{ m}^2 \text{ m}^{-2}$ for *Q. pyrenaica* stands located in Central–Western Spain. This values can be qualified as low or very low compared with LAI values reported for other congeneric species: 5.8 for *Q. petraea* (Davi et al. 2009), 5.0 for *Q. robur* (Chapter 4, this volume), 3.4 for *Q. cerris* (Llorens and Domingo 2007), 3.3 and $2.9 \text{ m}^2 \text{ m}^{-2}$ for *Q. pubescens* (Čermák et al. 1998; Damesin et al. 1998, respectively).

In a comparative study of 17 *Quercus* species (Corcuera et al. 2004), *Q. pyrenaica* shows values for some water-related parameters closer to Mediterranean evergreen

oaks than those of deciduous ones. For instance, *Q. pyrenaica* showed very low leaf water potential (Ψ_l) at the turgor-loss point ($\Psi_{\text{tlp}} < -3.2$ MPa), similar to other Mediterranean deciduous oaks (*Q. cerris* and *Q. frainetto*) and clearly lower than temperate deciduous ones (around -2.4 MPa). Osmoregulation is a strategy for drought tolerance, and *Q. pyrenaica* showed a low osmotic potential (π) at full turgor ($\pi_0 < -2.6$ MPa), again similar to other Mediterranean deciduous oaks and clearly lower than temperate deciduous ones (around -2 MPa). Finally, *Q. pyrenaica* showed a high maximum bulk modulus of elasticity ($\epsilon_{\text{max}} \approx 18$ MPa), the highest among the deciduous oaks. More inelastic tissues will result in a more rapid decrease of turgor with loss of water; this will generate a steeper soil to leaf water potential gradient and, consequently, less leaf dehydration. This may improve water uptake from dry soils, avoiding severe water deficit in leaf tissues, what is important for species with deep rooting as oaks. Their capacity of exploiting deep soil layers improves soil–water extraction, maintaining the soil to leaf water potential gradient without leaves becoming too much dehydrated (Aranda et al. 2004).

Study Area

Data used in this article are based on a long-term monitoring carried out in four *Q. pyrenaica* stands located in the *Sierra de Gata* ($40^\circ 2' 40''$ N, $3^\circ 0' 50''$ W, CW of Spain). Four stands are located in a smoothly hilly area along a rainfall gradient: 720, 872, 1,245 and 1,580 mm a^{-1} for S_{dry} , $S_{\text{m-dry}}$, $S_{\text{m-wet}}$ and S_{wet} , respectively. The climate is sub-humid Mediterranean according to the Emberger's climogram, with relatively high amount of annual rainfall and moderate temperatures (annual mean about 12°C). Soils are acid, predominantly *Cambisols* with a typical A-humic, B-weathering, and C-horizons (AhBwC profile) developed over granites, gneiss, schists, and greywackes.

From litterfall data (Gallardo et al. 1998) we have estimated LAI values ranging from 1.8 and $2.6 \text{ m}^2 \text{ m}^{-2}$ in the four *Q. pyrenaica* stands. These values are similar to those reported for other *Q. pyrenaica* stands (Hernández-Santana et al. 2008a).

Other characteristics of the four stands are given in Table 10.1.

Temporal Dynamic of Soil Moisture. Estimation of Stand Evapotranspiration

Soil water content (SWC), in terms of both extreme and mean values, increased gradually with soil depth throughout growing season (June–September). The minimum SWC was found at the surface, as expected, owing to a more marked drying process at the soil surface (Fig. 10.1). Increases in SWC at depth, with a certain delay over the more superficial horizons, were noticeable from the beginning autumn, i.e., the soil

Table 10.1 Characteristics of the four experimental *Q. pyrenaica* plots ('Sierra de Gata' Moutains, Spain)

	Characteristics	Units	Fuentegualdo (S _{dry})	Villasrubias (S _{n-dry})	El Payo (S _{m-wet})	Navasfrías (S _{wet})
t1.2	Geology (Paleozoic)		Granite	Schist	Granite	Schist
t1.3	Altitude	m a.s.l.	870	900	940	960
t1.4	Slope	%	2–5%	10–15%	5%	5–15%
t1.5	Mean annual temperature	°C	13.3	Not available	Not available	11.4
t1.6	Mean annual precipitation	mm	720	872	1,245	1,580
t1.7			Humic	Humic	Humic	Humic
t1.8	Soil units		Humic	Humic	Humic	Humic
t1.9	(ISSS-ISRIC-FAO 1998)		Cambisol	Cambisol	Cambisol	Cambisol
t1.10	Soil depth	cm	–85	–55	–125	–80
t1.11	Soil texture		Sandy-loam	Silt-loamy	Loamy	Silt-loamy
t1.12	AWC ^a soil	cm ³ cm ^{–3}	0.16	0.21	0.13	0.18
t1.13	AWC ^a bedrock	cm ³ cm ^{–3}	0.08	0.11	0.05	0.11
t1.14	Dominant understory		Shrubs	Shrubs	Grasses	Ferns
t1.15	Tree density	Tree ha ^{–1}	738	1,043	406	820
t1.16	LAI ^b	m ² m ^{–2}	2.6	2.0	1.9	1.8
t1.17	Tree DBH ^c	mm	165	110	254	152
t1.18	Tree height	m	12.0	8.5	17.0	13.0
t1.19	Tree age ^d	Years	80	60	80	60
t1.20	Basal area	m ² ha ^{–1}	21.2	13.5	19.9	15.6
t1.21	Last thinning	Years ago	35	25	50	35
t1.22	DBH increment	mm year ^{–1}	3.2	2.5	0.8	2.4
t1.23	Biomass ^e	Mg ha ^{–1}	98	63.8	131	64.5
t1.24	Production ^f	Mg ha ^{–1} year ^{–1}	4.19	2.85	3.52	2.6

^aAvailable soil water content^bLeaf Area index

Tree diameter at breast height

^dDominant tree height^cAboveground tree biomass

wetting front advanced very rapidly (data not shown). The pattern of soil profile dryness, similar throughout years and plots, showed a gradual change of the relative importance of the water at different depths (Fig. 10.1). Comparing SWC values of consecutive dates, it observed that at the beginning of the growing season, soil dry mostly in the uppermost soil layers, while dryness is a slow process at the deep layers. Over time, the deep soil water acquires higher relative importance; that is, SWC values decreases mostly at deep layers, indicating that only deep soil water is being consumed by plants.

The seasonal variation of SWC within the first 100 cm depth closely mirrored the precipitation pattern, with alternating wet and dry periods occurring in all stands and years analysed (Fig. 10.2). Autumn recharge entailed a rapid soil

Fig. 10.1 Temporal evolution of soil drying in *Quercus pyrenaica* forests of Central-Western Spain. More examples, including soil re-watering period, in Moreno et al. (1996), Vicente et al. (2003)

Fig. 10.2 Temporal course of soil water content (0–100 cm depth; SWC), precipitation (P), potential evapotranspiration (E_p) and actual evapotranspiration (E_A) in a *Quercus pyrenaica* forests of Central-Western Spain (Adapted from Moreno et al. (1996) and Vicente et al. (2003)

moistening, obtaining frequently maximum values of SWC at the end of autumn. Although in dry autumn, complete soil recharge was reached later, it was reached every year. Then, SWC content remained more or less constant till mid spring, when soil begun to dry quickly. Some years, when trees leafed out (end May–early June) more than 50% of the available water content (AWC) had been consumed and, every year, AWC practically was exhausted halfway through the summer. Then the soil remained similarly dry during 30–50 days, with the exception of some abnormally wet summer. The situation of water deficit occurred earlier and lasted longer at the dry sites, but minimum SWC values are similar for each plot every year. On average, SWC declined from the bud burst to the end of the summer by 115 mm in S_{wet} , 111 mm in S_{m-wet} , 113 mm in S_{m-dry} , and 79 mm in S_{dry} , differences being more related with soil depth and texture, than rainfall amounts (Table 10.1).

From the temporal evolution of SWC, monthly actual evapotranspiration (E_A) of the four stands was calculated by applying a simple iterative model of monthly water balance (Moreno et al. 1996). The model is based on the relationship between deep drainage (water flowing down from the soil to the bedrock; D_p) and SWC, and on the limitation imposed by E_p (potential evapotranspiration). These authors found that P was significantly related to D_p but not to E_A . The higher P values in wet and cold season were, the higher D_p values were, without involving a significant change in the water availability for plants. Rainfall interception was moderate and surface runoff negligible (15 and <0.5% of the rainfall, respectively). The limited SWR determined moderate to low E_A rates in the growing season (Table 10.2) and with

Table 10.2 Mean values of precipitation (P), actual evapotranspiration (E_A), and ratios of actual and potential evapotranspiration (E_A/E_p) in four *Q. pyrenaica* stands located along a rainfall gradient (wet, moderately wet, moderately dry and dry sites). Data refer consecutive growing seasons (May–September)

Growing season	Water flow	Experimental sites				
		S_{wet}	S_{m-wet}	S_{m-dry}	S_{dry}	
1990	P	207	184	179	137	t2.6
	E_A	180	202	193	159	t2.7
	E_A/E_p	0.29	0.32	0.31	0.25	t2.8
1991	P	114	104	107	82	t2.9
	E_A	205	178	213	154	t2.10
	E_A/E_p	0.34	0.29	0.34	0.24	t2.11
1992	P	347	272	244	173	t2.12
	E_A	216	209	208	167	t2.13
	E_A/E_p	0.37	0.35	0.35	0.27	t2.14
1993	P	562	422	407	342	t2.15
	E_A	261	256	278	239	t2.16
	E_A/E_p	0.48	0.46	0.49	0.42	t2.17
Average	P	308	246	234	183	t2.18
	E_A	216	211	223	180	t2.19
	E_A/E_p	0.37	0.36	0.37	0.30	t2.20

scarce differences among plots. E_A differs significantly only among S_{dry} and the rest of stands, because of the lower P and SWC of the former site. Maximum E_A value was usually found in June, and August usually showed the lowest mean values. The E_A values (mm day^{-1}) for August ranged from 0.40 to 0.97 for S_{wet} , 0.74 to 0.87 for S_{m-wet} , 0.74 to 0.90 for S_{m-dry} , and 0.37 to 0.80 for S_{dry} . According to the low E_A values, it should seem that *Q. pyrenaica* trees experienced a strong water deficit, with mean E_A/E_p ratios ranging, on average, from 0.30 to 0.37 in the growing season (0.14–0.28 in August).

Daily and Seasonal Evolution of Stomata Activity. Estimating Tree Transpiration

Studies carried out in two extremes of the rainfall gradient (S_{wet} and S_{dry}) showed that trees maintained very favourable water conditions throughout summer, with predawn leaf water potential (Ψ_{l-pd}) very high at two sites in two consecutive summers (Fig. 10.3). Only 1 day of the 18 monitored, the Ψ_{l-pd} was < -1 MPa (Gallego et al. 1994). Similarly, Hernández-Santana et al. (2008a) found $\Psi_{l-pd} < -1$ MPa only 1 day from a total of 24 days monitored (2004–2006) in different *Q. pyrenaica* stands, while evergreen-oak forests frequently reach Ψ_{l-pd} values around -4 MPa (Savé et al. 1999).

Ψ_{l-pd} correlated better with the seasonal dynamics of SWC of the deepest layers (60–100 cm soil depth; Gallego et al. 1994). Differences between wet and dry sites were only found at the end of the driest summer. Leaf water potential (Ψ_l) decreased quickly during the day with the minimum value early in the afternoon, but it remained the whole time above the turgor-loss point (-3.2 MPa; Corcuera et al. 2002). In the afternoon, Ψ_l increased also quickly, and at the sunset values similar to Ψ_{l-pd} has been reached (Fig. 10.3).

Despite the rapid decrease of Ψ_l , stomatal conductance (g_s) was high in all monitored days (Fig. 10.4). Maximum mean values of g_s (around $250 \text{ mmol m}^{-2} \text{ s}^{-1}$) and mean daily values varied very little along summer (Fig. 10.4), in spite of the fact that SWR was depleted. The diurnal behaviour of stomatal activity (g_s) indicated the absence of limiting factors most of the summers; g_s increased in the morning and reached a maximum about 3 h before the daily minimum in Ψ_l occurred. Maximum g_s values were reached at wet site (S_{wet}), but daily curves showed a more quick and acute decreased of g_s along day at S_{wet} , defining a stronger effect of water deficit at S_{wet} than at S_{dry} .

Stomata conductance behaviour with respect to atmospheric humidity may be linear or nonlinear, depending on the type of control mechanism. Rico et al. (1996) showed for S_{wet} and S_{dry} stands that stomata conductance of *Q. pyrenaica* remained constant at low and moderate vapour pressure deficit (VPD) and strongly decreased after a VPD threshold (2.4 kPa). This response is interpreted in terms of high sensitivity to drought and weak functional adaptative strategy of trees, similarly to other deciduous *Quercus* (Chambers et al. 1985). This decrease of g_s with VPD was

Fig. 10.3 Daily curve of leaf water potential (Ψ_l) in some selected days of summer 1991 (top) and seasonal evolution of predawn leaf water potential (Ψ_{l-pd}) along summers 1991 and 1992 (bottom) at two *Quercus pyrenaica* stands (dry and wet; Adapted from Gallego et al. 1994)

Fig. 10.4 Daily curves of stomatal conductance (g_s) at two *Quercus pyrenaica* stands (dry and wet) along summer 1991 (Adapted from Gallego et al. 1994)

more attenuated, but began earlier (lower VPD), at the drier site. Here g_s showed a more linear tendency, typical of species adapted to aridity, with a conservative strategy. g_s showed also little response to Ψ_l , remaining high in certain range of Ψ_l . After a threshold (Ψ_l around -2 MPa) a rapid decrease in g_s occurred as potential continued to decline. Winkel and Rambal (1990) detected similar response in other deciduous oaks. Differences between dry and wet sites were again detected, although less acute than for g_s response to VPD. A better response of g_s to Ψ_l was detected in dry site, with a high threshold and a less pronounced trend than in wet site (Rico et al. 1996).

From seasonal and diurnal curves of g_s values, VPD and LAI data, E_A was estimated for S_{dry} and S_{wet} stands. Estimation also involved the calculation of the decoupling coefficient (Ω) of Jarvis and McNaughton (1986), which is a measure of the coupling between conditions at the canopy surface and in the free air stream. For the study stands and days, we have estimated Ω values moderately high (0.34 on average), as a result of large stomata and low wind velocities. This value indicated a rather low stomata control of transpiration (which grows progressively weaker as Ω approaches 1.0) if compared with other broadleaf forests (Jarvis and McNaughton 1986; Goldberg and Bernhofer 2008).

Values of E_A , so estimated, do not show a clear seasonal trend or clear differences between sites; values ranged 2–4 mm day⁻¹ (Fig. 10.5). Recently, Hernández-Santana et al. (2008b) also reported values of daily E_A above 2 mm for most of the summer days in similar *Q. pyrenaica* forest stands. E_A values here estimated are threefold higher than those estimated from soil water balance. Although both approaches of E_A estimation have a certain level of uncertainty, the high differences must be, a least partially, explained because of the existence of an additional source of water for tree transpiration that is not accounted in the soil water balance.

Fig. 10.5 Mean values of daily actual evapotranspiration (E_A) in two (dry and wet sites) estimated from stomata conductance (g_s) and from time course of soil water content (SWC)

Lessons Learn252

Quercus pyrenaica Oak Is Only Slightly Water-Limited253
During Summer Drought254

In response to progressive decreases in soil water, no substantial changes were255
found in Ψ_l or in g_s , with a tendency to use up water reserves from progressively256
deeper soil layers, thereby avoiding marked stomata closure. *Q. pyrenaica* seems257
well adapted to surviving summer drought period while maintaining photosynthetic258
activity and it seems to have a non-conservative strategy of water consumption259
(sense Jones 1992), according to patterns described by other authors for different260
deciduous oaks (Mediavilla and Escudero 2003; Manes et al. 2006). Ψ_l and g_s of261
Q. pyrenaica remained high when SWR had been completely depleted. Tree trans-262
piration (E_A) only decreased slightly during summer in dry and wet stands of263
'Sierra de Gata' mountains and other stands of Central–Western Spain (Hernández-264
Santana et al. 2008b). However, stand E_A estimated from the soil water balance265
gave values much lower than those estimated from the leaf conductance, in spite of266
the fact that the latter only included tree transpiration and the former included soil267
evaporation (presumably negligible) and understorey (shrubs and grasses) transpi-268
ration, besides the tree transpiration. Irrespective of possible imprecision on E_A 269
estimates, differences among both approaches allow speculating that trees take up270
water from an extra water reserve.271

Quercus pyrenaica Oaks Depend on Thick Porous-Weathered272
Bedrocks273

The ability to take up water stored in the upper few meters of the weathered bedrock274
during the pronounced dry season is likely the key feature allowing *Q. pyrenaica* to275
thrive under dry summer conditions in the shallow, rocky soils of study sites, as other276
authors have shown for other Mediterranean-type ecosystems (Sternberg et al. 1996;277
Witty et al. 2003; Schiller et al. 2007). Although weathered bedrock has much lower278
available-water capacities in the four *Q. pyrenaica* stands than those of soils279
(Table 10.1), the weathered rock zone is much thicker (several meters) than the soil280
(< -1 m). From our data, we estimated that a hydraulically active bedrock of around281
 -2.2 and -4.8 m depth (on schist and granite soils, respectively, derived of old282
weathering during the last interglacial periods; Gallardo and Molina 1979) can pro-283
vide the water needed by *Q. pyrenaica* trees during summer in the study area. Witty284
et al. (2003) reported that weathered bedrock supplied at least 70% of the water used285
by the *Pinus jeffreyi* during the growing season in Sierra Nevada mountains, USA.286
The scarce information available on the *Quercus pyrenaica* rooting system indicates287
a rapid decrease of root length density with depth (Schneider et al. 2001) and also288

Fig. 10.6 Variation in SWC at three depths from June to September 2006 and 2007 in a *Q. pyrenaica* stands in Central–Western Spain (Adapted from Hernández-Santana et al. 2008b)

that most of the root is located in the first –50 cm of the soil (Hernández-Santana et al. 2008a). However, deep rooting has been suggested to be a key trait to overcome water depletion in the upper soil layers during the dry season in Mediterranean ecosystems (Rambal 1984; David et al. 2004; Kurz-Besson et al. 2006; Querejeta et al. 2007). Indeed, Cubera and Moreno (2007) and Hernández-Santana et al. (2008b) have shown that *Q. ilex* and *Q. pyrenaica* stands of Central–Western Spain use soil water located deeper than –2.5 m depth (Fig. 10.6).

A complete re-moistening of thick bedrocks in wet season needs of high rates of water infiltration and non-torrential rainfall regimes. However, rainfall regime seems to be changing and less frequent and more torrential rainfall events are predicted for the near future in Mediterranean Basin (IPCC 2007). Through a decadal analysis of the rainfall over the last 55 years, Hernández-Santana et al. (2008a) have shown a decrease of mean annual rainfall of 17.7%. This trend was more marked in summers (decrease of 26.1%). This trend could reduce adequate bedrock re-watering in the forthcoming years and water stress experienced by *Q. pyrenaica* would be more pronounced. For instance, Mediavilla and Escudero (2003) found Ψ_{l-pd} values as low as –3.2 MPa where thick weathered bedrock was not present.

Quercus pyrenaica Is a Well-Performed Deciduous Oak to Cope with Increasing Summer Drought

Morphological (e.g., low LAI) and physiological (e.g., low Ψ_{tlp} and π_o , and high ε_{max}) differences between *Q. pyrenaica* and other deciduous oaks will be surely crucial under this global change scenario. E_A values here reported and those reported by Hernández-Santana et al. (2008a) for *Q. pyrenaica* can be qualified as moderately low. E_A rates always showed an upper limit well below E_p , indicating

a control of transpiration by stomata (Rico et al. 1996; Hernández-Santana et al. 2008b). The fact that transpiration becomes constant above a certain threshold of VPD, with a gradual stomata closure as VPD increases, protects xylem from catastrophic cavitations (David et al. 2004; Chapter 3, this volume).

Stomata activity and its response to atmospheric conditions varied clearly between sites (Rico et al. 1996). With favourable water availability, wet sites reached higher conductance values, although stomata functioning fell off sharply starting with a threshold value, mainly VPD and Ψ_l . Under dry conditions, more homogeneous conductance values are found, with a less pronounced but more immediate and constant response to environmental variability (Rico et al. 1996). This could be interpreted as a functional adaptation, implying a more conservative strategy of *Q. pyrenaica* growing in drier sites. This possible genetic differentiation will require further studies given its potential interest for future forest dynamic under increasing water deficit in Mediterranean and temperate forests in Europe.

References

- Aranda I, Gil L, Pardos JA (2004) Osmotic adjustment in two temperate oak species [*Quercus pyrenaica* Willd and *Quercus petraea* (Matt.) Liebl] of the Iberian Peninsula in response to drought. Invest Agrar: Sist Recur For 13:339–345
- Baldocchi DD, Liukang X (2007) What limits evaporation from Mediterranean oak woodlands – the supply of moisture in the soil, physiological control by plants or the demand by the atmosphere? Adv Water Resour 30:2113–2122
- Blake-Jacobson ME (1987) Stomatal conductance and water relations of shrubs growing at the chaparral-desert ecotone in California and Arizona. In: Tenhunen JD, Catarino EM, Lange OL, Oechel WC (eds) Plant responses to stress. Functional analysis in Mediterranean ecosystems, vol G15, Nato ASI Ser. Springer Verlag, Berlin, pp 223–245
- Bréda N, Huc R, Garnier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of eco-physiological responses, adaptation processes and long-term consequences. Ann For Sci 63:625–644
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595
- Čermák J, Nadezhdina N, Raschi A, Tognetti R (1998) Sap flow in *Quercus pubescens* and *Quercus cerris* stands in Italy. In 4th International workshop on measuring sap flow in intact plants. IUFRO Publications, Mendel University, Zidlochovice, Czech Republic
- Chambers JL, Hinkley TM, Cox GS, Metcalf CL, Aslin RG (1985) Boundary-line analysis and models of leaf conductance for four oak-hickory forest species. For Sci 3:437–450
- Ciais Ph, Reichstein M, Viovy N, Granier A, Ogeé J, Allard V, Aubinet M, Buchmann N, Chr B, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2003) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533
- Corcuera L, Camarero J, Gil-Pelegrín E (2002) Functional groups in *Quercus* species derived from the analysis of pressure–volume curves. Trees 16:465–472
- Corcuera L, Camarero J, Gil-Pelegrín E (2004) Effects of a severe drought on *Quercus ilex* radial growth and xylem anatomy. Trees 18:83–92

- Cubera E, Moreno G (2007) Effect of single *Quercus ilex* trees upon spatial and seasonal changes in soil water content in Dehesas of central western Spain. *Ann For Sci* 64:355–364
- Damesin C, Rambal S, Joffre R (1998) Cooccurrence of trees with different leaf habit: a functional approach on Mediterranean oaks. *Acta Oecol* 18:195–204
- Davi H, Barbaroux C, Francois C, Dufrêne E (2009) The fundamental role of reserves and hydraulic constraints in predicting LAI and carbon allocation in forests. *Agr For Meteorol* 149:349–361
- David TS, Ferreira MI, Cohen S, Pereira JS, David JS (2004) Constraints on transpiration from an evergreen oak tree in southern Portugal. *Agric For Meteorol* 122:193–205
- Duhme F, Hinchley TM (1992) Daily and seasonal variation in water relations of macchia shrubs and trees in France (Montpellier) and Turkey (Antalya). *Vegetatio* 99–100:185–198
- Gallardo JF (2000) Biogeochemistry of Mediterranean forest ecosystems: a case study. In: Bollag JM, Stotzky G (eds) *Soil biochemistry*. Marcel Dekker, New York, pp 423–460
- Gallardo JF, Martín A, Santa-Regina I (1998) Nutrient cycling in deciduous forest ecosystems of the 'Sierra de Gata' mountains: aboveground litter production and potential nutrient return. *Ann Sci For* 55:749–769
- Gallardo JF, Molina E (1979) Relaciones entre procesos edáficos y superficies morfológicas de la Cuenca Duero, vol 1, *Actas I Reunión Geológica*. Salamanca, Spain, pp 211–223
- Gallego HA, Rico M, Moreno G, Santa Regina I (1994) Leaf water potential and stomatal conductance in *Quercus pyrenaica* Willd forests: vertical gradients and response to environmental factors. *Tree Physiol* 14:1039–1047
- Goldberg V, Bernhofer C (2008) Testing different decoupling coefficients with measurements and models of contrasting canopies and soil water conditions. *Ann Geophys* 26:1977–1992
- Grier CC, Running SW (1977) Leaf area of mature northwestern coniferous forests: relation to the site water balance. *Ecology* 58:893–899
- Hernández-Santana V, David TS, Martínez-Fernández J (2008a) Environmental and plant-based controls of water use in a Mediterranean oak stand. *For Ecol Manag* 255:3707–3715
- Hernández-Santana V, Martínez-Fernández J, Morán C, Cano A (2008b) Response of *Quercus pyrenaica* (melojo oak) to soil water deficit: a case study in Spain. *Eur J For Res* 127:369–378
- IPCC (2007) *Climate change 2007: the physical scientific basis*. Cambridge University Press, Cambridge, UK, 1009 pp
- ISSS-ISRIC-FAO 1998. *World Reference Base for Soil Resources*. World Soil Resources, Reports No. 84. FAO UN, Rome, 1998
- Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. *Adv Ecol Res* 15:1–49
- Jones HG (1992) *Plants and microclimate. A quantitative approach to environmental plant physiology*. Cambridge University Press, Cambridge
- Kurz-Besson C, Otieno D, Lobo do Vale R, Siegwolf R, Schmidt M, Herd A, Nogueira C, David T, David J, Tenhunen J, Pereira J, Chaves M (2006) Hydraulic lift in cork oak trees in a savannah-type Mediterranean ecosystem and its contribution to the local water balance. *Plant Soil* 282:361–378
- Llorens P, Domingo F (2007) Rainfall partitioning by vegetation under Mediterranean conditions. A review of studies in Europe. *J Hydrol* 335:37–54
- Manes F, Vitale M, Donato E, Giannini M, Puppi G (2006) Different ability of three Mediterranean oak species to tolerate progressive water stress. *Photosynthetica* 44:387–393
- Martínez-Vilalta J, Piñol J, Beven K (2002) A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. *Ecol Model* 155:127–147
- Mediavilla S, Escudero A (2003) Stomata l responses to drought at a Mediterranean site: a comparative study of co-occurring woody species differing in leaf longevity. *Tree Physiol* 23:987–996
- Merino J, Field C, Mooney HA (1982) Construction and maintenance costs of Mediterranean-climate evergreen and deciduous leaves. I. Growth and CO₂ exchange analysis. *Oecologia* 53:208–213
- Moreno G, Gallardo JF, Ingelmo F, Cuadrado S, Hernández J (1996) Soil water budget in 4 *Quercus pyrenaica* forests across a rainfall gradient. *Arid Soil Res Rehabil* 10:65–84
- Moreno G, Obrador JJ, Cubera E, Dupraz C (2005) Root distribution in dehesas of Central-Western Spain. *Plant Soil* 277:153–162

- Ogaya R, Peñuelas J (2007) Leaf mass per area ratio in *Quercus ilex* leaves under a wide range of climatic conditions. The importance of low temperatures. *Acta Oecol* 31:168–173
- Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biol* 9:131–140
- Peñuelas J, Lloret F, Montoya R (2001) Severe drought effects on Mediterranean woody flora in Spain. *For Sci* 47:214–218
- Querejeta JJ, Egerton-Warburton LM, Allen MF (2007) Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California oak savanna. *Soil Biol Biochem* 39:409–417
- Rambal S (1984) Water balance and pattern of root water uptake by a *Quercus coccifera* L. evergreen scrub. *Oecologia* 62:18–25
- Rambal S (1993) The differential role of mechanisms for drought resistance in a Mediterranean evergreen shrub: a simulation approach. *Plant Cell Environ* 16:35–44
- Rico M, Gallego HA, Moreno G, Santa Regina I (1996) Stomata l response of *Quercus pyrenaica* to environmental factors in 2 sites differing in their annual rainfall (Sierra de Gata, Spain). *Ann For Sci* 53:221–234
- Rodá F, Retana J, Gracia CA, Bellot J (1999) Ecology of Mediterranean evergreen oak forests. Springer, Berlin, p 373
- Savé R, Castell C, Terradas J (1999) Gas exchange and water relations. In: Rodá F, Retana J, Gracia CA, Bellot J (eds) Ecology of Mediterranean evergreen oak forests, Ecological Studies, vol 137. Springer, Berlin, pp 135–144
- Schiller G, Cohen S, Ungar ED, Moshe Y, Herr N (2007) Estimating water use of sclerophyllous species under East-Mediterranean climate III. Tabor oak forest sap flow distribution and transpiration. *For Ecol Manag* 238:147–155
- Schneider K, Turrión MB, Grierson PF, Gallardo JF (2001) Phosphatase activity, microbial phosphorus, and fine root growth in forest soils in the ‘Sierra de Gata’, western central Spain. *Biol Fertil Soils* 34:151–155
- Silla F, Escudero A (2006) Coupling N cycling and N productivity in relation to seasonal stress in *Quercus pyrenaica* Willd. samplings. *Plant Soil* 282:301–311
- Sobrado MA (1986) Aspects of tissue water relations and seasonal changes of leaf water potential components of evergreen and deciduous species coexisting in tropical dry forest. *Oecologia* 68:413–416
- Sternberg PD, Anderson MA, Graham RC, Beyers JL Tice KR (1996) Root distribution and seasonal water status in weathered granitic bedrock under chaparral. *Geoderma* 72:89–98
- Valladares F, Peñuelas J, De Luis-Calabuig E (2004) Impactos sobre los ecosistemas terrestres. In: Moreno JM (Coord) Evaluación Preliminar de los impactos en España del cambio climático (ECCE). Ministerio de Medio Ambiente, Madrid, pp 65–112
- Vicente MA, Gallardo JF, Moreno G, González MI (2003) Comparison of soil water-contents as measured with a neutron probe and time domain reflectometry in a Mediterranean forest (‘Sierra de Gata’, Central Western Spain). *Ann For Sci* 60:185–193
- Winkel T, Rambal S (1990) Stomata l conductance of some grapevines growing in the field under a Mediterranean environment. *Agric For Meteorol* 51:107–121
- Witty JH, Graham RC, Hubbert KR, Doolittle JA, Wald JA (2003) Contributions of water supply from the weathered bedrock zone to forest soil quality. *Geoderma* 114:389–400

Author Query

Chapter No.: 10 0001196708

Query	Details Required	Author's Response
AU1	Please check if the running head can be deleted from the COP to maintain consistency among other chapters.	

Uncorrected Proof