

# 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	<b>Gerardo</b>
	Suffix	
	Division	Forestry School
	Organization	University of Extremadura
	Address	10600, Plasencia, Spain
	Email	gmoreno@unex.es
Author	Family Name	Gallardo
	Particle	
	Given Name	<b>Juan F.</b>
	Suffix	
	Division	
	Organization	CSIC, I.R.N.A.
	Address	37071, Salamanca, Spain
	Email	
Author	Family Name	Vicente
	Particle	
	Given Name	<b>María Ángeles</b>
	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 basin and that drought episodes could be more frequent in the present century due to climate change (IPCC 2007). Similar changes are also expected in temperate regions in the Northern Europe (Bréda et al. 2006) and South-Eastern Europe (Chapter 8, this volume), with direct consequences on forest health. A massive dieback of oaks forest (both evergreen and deciduous) has been observed some summers in last decades (Peñuelas et al. 2001; Corcuera et al. 2004), and several authors have shown how some mesic Mediterranean trees could be replaced for other more xeric species under the current scenario of climate change in Mediterranean forests (Martínez-Vilalta et al. 2002; Peñuelas and Boada 2003). 9-18

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 a scenario of climate change (Baldocchi and Liukang 2007). The genus *Quercus* comprises 531 tree and shrub species distributed among contrasting phytoclimates in the Northern Hemisphere, from temperate and subtropical deciduous forests to dry Mediterranean evergreen woodlands (Corcuera et al. 2002). The range of variation in the ecophysiology of Mediterranean oaks is comparable to that observed between other deciduous and 19-26

---

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

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

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

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

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

64 Stomata regulation is considered the most immediate mechanism of the optimi-  
65 sation of C-gain/water-loss in plants (Rambal 1993) and we hypothesised that  
66 deciduous trees exhibit a non-conservative pattern of water transpiration (stomata  
67 activity), contrary to their neighbour or co-existing evergreen trees (Damesin et al.  
68 1998). The reduction of leaf area index (LAI) is a third mechanism associated to  
69 optimisation of WUE and, presumably, Mediterranean deciduous oaks have low  
70 LAI compared to congeneric species, either temperate deciduous or Mediterranean  
71 evergreen oaks.

Given the wealth of information that exists on water dynamics of temperate 72  
coniferous and deciduous broadleaves (e.g., Bréda et al. 2006), and Mediterranean 73  
evergreen trees and forests (e.g., Rodá et al. 1999; Ciais et al. 2003), corresponding 74  
knowledge is scarce about Mediterranean deciduous species. The understanding of 75  
these southern deciduous forests is needed for modelling water budgets and water 76  
yield, planning forest conservation and/or restoration programmes, and understanding 77  
the future dynamic of both Mediterranean and temperate forests under current 78  
scenarios of climate change. 79

In this article we analyse how a Mediterranean deciduous oak, *Quercus pyre-* 80  
*naica*, with a short vegetative period coincident with summer drought, cope with 81  
water deficit in that period. We revised published data on temporal dynamic of soil 82  
moisture and physiological status of tree leaves of several forest stands of Central– 83  
Western Spain and discuss the significance of soil water reserve (SWR) and deep 84  
rooting system on the maintenance of tree transpiration and physiological activity 85  
of the trees along summer drought. Accordingly, the following three questions are 86  
addressed: (a) Are trees water-limited during summer drought? (b) What is the tree 87  
water source during summer drought? and (c) Which adaptative mechanisms 88  
exhibit this species to face water deficit? 89

## Study Species 90

*Quercus pyrenaica* is a slow-growing Mediterranean deciduous species, distributed 91  
throughout mountainous sub-humid Mediterranean areas of the southwestern 92  
region of Europe, especially in the western regions of the Iberian Peninsula. It has 93  
a short growing season (from the end of May till mid October), which may deter- 94  
mine its distribution. The species is well adapted to survive maintaining photosyn- 95  
thetic production in spite of the long summer water deficit (Gallego et al. 1994; 96  
Rico et al. 1996) and, therefore, it often occupies transitional areas from sub-humid 97  
to semi-arid conditions (Hernández-Santana et al. 2008a). Despite its distribution 98  
and interesting ecology, *Q. pyrenaica* has been poorly studied in comparison with 99  
other Mediterranean *Quercus* species (Silla and Escudero 2006), probably because 100  
of its low aboveground productivity (Gallardo 2000). 101

A common strategy to thrive on water-limited conditions is the reduction of the 102  
transpiration area (Rambal 1993); then, leaf area index (LAI) usually decreases 103  
with water deficit (Grier and Running 1977; Ogaya and Peñuelas 2007). Hernández- 104  
Santana et al. (2008a) have reported an average value of 2.4 m<sup>2</sup> m<sup>-2</sup> for *Q. pyrenaica* 105  
stands located in Central–Western Spain. This values can be qualified as low or 106  
very low compared with LAI values reported for other congeneric species: 5.8 for 107  
*Q. petraea* (Davi et al. 2009), 5.0 for *Q. robur* (Chapter 4, this volume), 3.4 for *Q.* 108  
*cerris* (Llorens and Domingo 2007), 3.3 and 2.9 m<sup>2</sup> m<sup>-2</sup> for *Q. pubescens* (Čermák 109  
et al. 1998; Damesin et al. 1998, respectively). 110

In a comparative study of 17 *Quercus* species (Corcuera et al. 2004), *Q. pyrenaica* 111  
shows values for some water-related parameters closer to Mediterranean evergreen 112

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

## 129 Study Area

130 Data used in this article are based on a long-term monitoring carried out in four *Q.*  
131 *pyrenaica* stands located in the *Sierra de Gata* ( $40^\circ 2' 40''$  N,  $3^\circ 0' 50''$  W, CW of  
132 Spain). Four stands are located in a smoothly hilly area along a rainfall gradient:  
133 720, 872, 1,245 and 1,580 mm  $\text{a}^{-1}$  for  $S_{\text{dry}}$ ,  $S_{\text{m-dry}}$ ,  $S_{\text{m-wet}}$  and  $S_{\text{wet}}$ , respectively. The  
134 climate is sub-humid Mediterranean according to the Emberger's climogram, with  
135 relatively high amount of annual rainfall and moderate temperatures (annual mean  
136 about  $12^\circ\text{C}$ ). Soils are acid, predominantly *Cambisols* with a typical *A*-humic,  
137 *B*-weathering, and *C*-horizons (AhBwC profile) developed over granites, gneiss,  
138 schists, and greywackes.

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

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

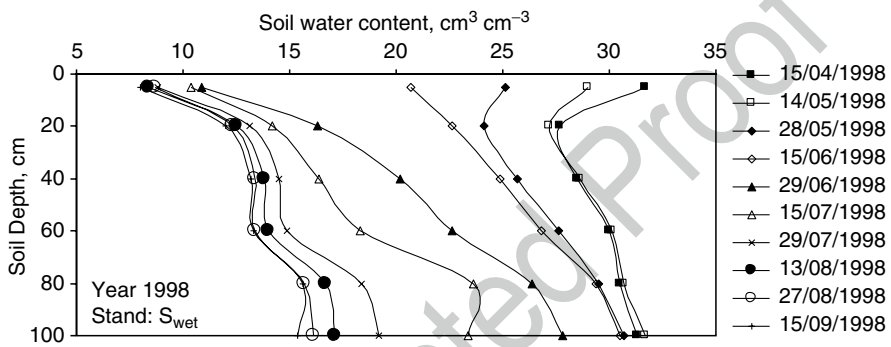
## 143 Temporal Dynamic of Soil Moisture. Estimation of Stand 144 Evapotranspiration

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

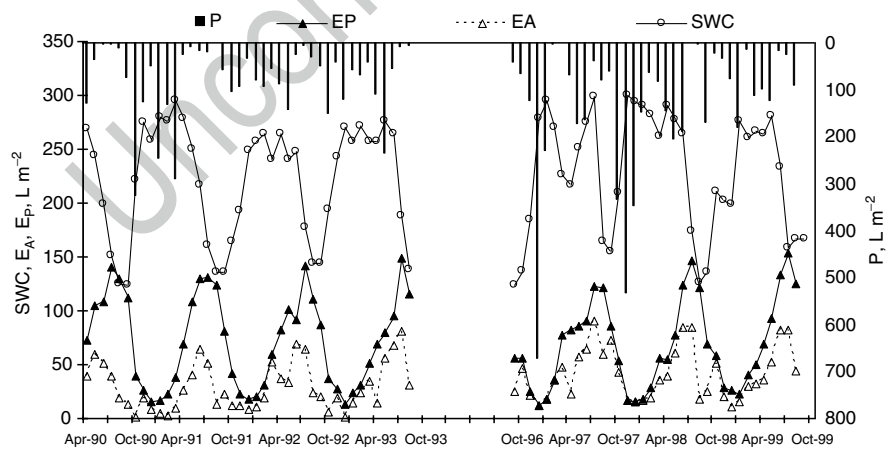


150 wetting front advanced very rapidly (data not shown). The pattern of soil profile  
 151 dryness, similar throughout years and plots, showed a gradual change of the relative  
 152 importance of the water at different depths (Fig. 10.1). Comparing SWC values of  
 153 consecutive dates, it observed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

158 The seasonal variation of SWC within the first 100 cm depth closely mirrored  
 159 the precipitation pattern, with alternating wet and dry periods occurring in all  
 160 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	t2.1
	$E_A$	180	202	193	159	t2.2
	$E_A/E_p$	0.29	0.32	0.31	0.25	t2.3
1991	$P$	114	104	107	82	t2.4
	$E_A$	205	178	213	154	t2.5
	$E_A/E_p$	0.34	0.29	0.34	0.24	t2.6
1992	$P$	347	272	244	173	t2.7
	$E_A$	216	209	208	167	t2.8
	$E_A/E_p$	0.37	0.35	0.35	0.27	t2.9
1993	$P$	562	422	407	342	t2.10
	$E_A$	261	256	278	239	t2.11
	$E_A/E_p$	0.48	0.46	0.49	0.42	t2.12
Average	$P$	308	246	234	183	t2.13
	$E_A$	216	211	223	180	t2.14
	$E_A/E_p$	0.37	0.36	0.37	0.30	t2.15



184 scarce differences among plots.  $E_A$  differs significantly only among  $S_{dry}$  and the rest  
 185 of stands, because of the lower P and SWC of the former site. Maximum  $E_A$  value  
 186 was usually found in June, and August usually showed the lowest mean values. The  
 187  $E_A$  values ( $\text{mm day}^{-1}$ ) for August ranged from 0.40 to 0.97 for  $S_{wet}$ , 0.74 to 0.87 for  
 188  $S_{m-wet}$ , 0.74 to 0.90 for  $S_{m-dry}$ , and 0.37 to 0.80 for  $S_{dry}$ . According to the low  $E_A$   
 189 values, it should seem that *Q. pyrenaica* trees experienced a strong water deficit,  
 190 with mean  $E_A/E_p$  ratios ranging, on average, from 0.30 to 0.37 in the growing season  
 191 (0.14–0.28 in August).

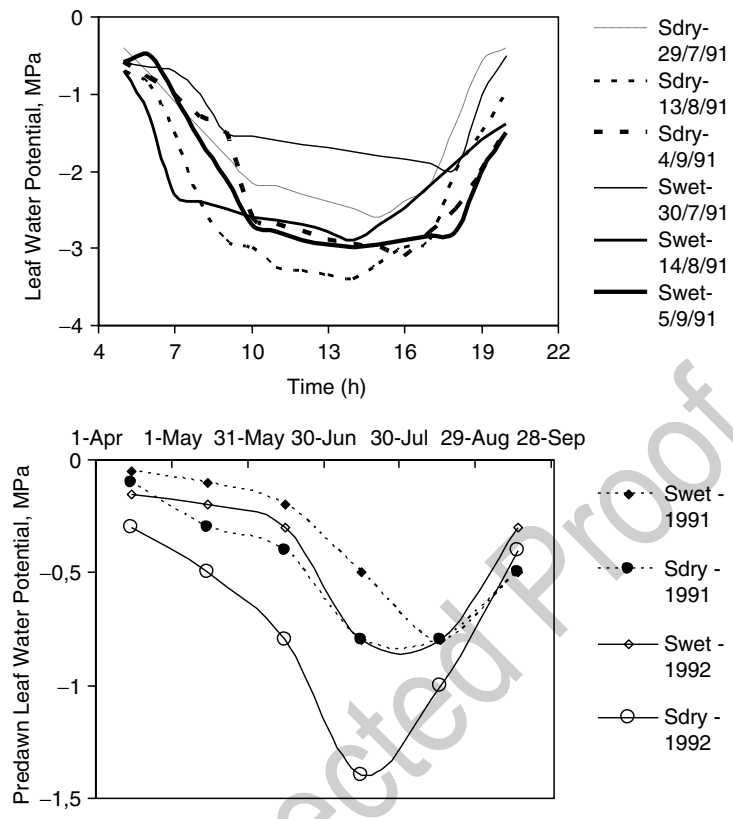
## 192 Daily and Seasonal Evolution of Stomata Activity. Estimating 193 Tree Transpiration

194 Studies carried out in two extremes of the rainfall gradient ( $S_{wet}$  and  $S_{dry}$ ) showed  
 195 that trees maintained very favourable water conditions throughout summer, with  
 196 predawn leaf water potential ( $\Psi_{l-pd}$ ) very high at two sites in two consecutive sum-  
 197 mers (Fig. 10.3). Only 1 day of the 18 monitored, the  $\Psi_{l-pd}$  was  $< -1$  MPa (Gallego  
 198 et al. 1994). Similarly, Hernández-Santana et al. (2008a) found  $\Psi_{l-pd} < -1$  MPa only  
 199 1 day from a total of 24 days monitored (2004–2006) in different *Q. pyrenaica*  
 200 stands, while evergreen-oak forests frequently reach  $\Psi_{l-pd}$  values around  $-4$  MPa  
 201 (Savé et al. 1999).

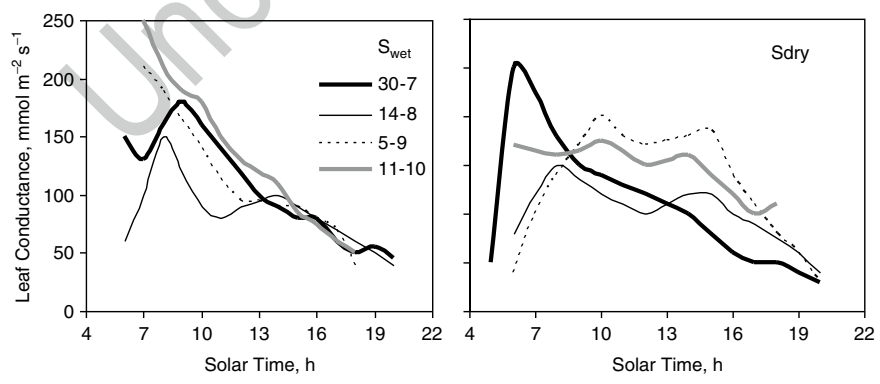
202  $\Psi_{l-pd}$  correlated better with the seasonal dynamics of SWC of the deepest layers  
 203 (60–100 cm soil depth; Gallego et al. 1994). Differences between wet and dry sites  
 204 were only found at the end of the driest summer. Leaf water potential ( $\Psi_l$ ) decreased  
 205 quickly during the day with the minimum value early in the afternoon, but it  
 206 remained the whole time above the turgor-loss point ( $-3.2$  MPa; Corcuera et al.  
 207 2002). In the afternoon,  $\Psi_l$  increased also quickly, and at the sunset values similar  
 208 to  $\Psi_{l-pd}$  has been reached (Fig. 10.3).

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

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



**Fig. 10.3** Daily curve of leaf water potential ( $\Psi_l$ ) in some selected days of summer 1991 (top) and seasonal evolution of predawn leaf water potential ( $\Psi_{l-pd}$ ) 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)

225 more attenuated, but began earlier (lower VPD), at the drier site. Here  $g_s$  showed a  
 226 more linear tendency, typical of species adapted to aridity, with a conservative  
 227 strategy.  $g_s$  showed also little response to  $\Psi_1$ , remaining high in certain range of  $\Psi_1$ .  
 228 After a threshold ( $\Psi_1$  around  $-2$  MPa) a rapid decrease in  $g_s$  occurred as potential  
 229 continued to decline. Winkel and Rambal (1990) detected similar response in other  
 230 deciduous oaks. Differences between dry and wet sites were again detected,  
 231 although less acute than for  $g_s$  response to VPD. A better response of  $g_s$  to  $\Psi_1$  was  
 232 detected in dry site, with a high threshold and a less pronounced trend than in wet  
 233 site (Rico et al. 1996).

234 From seasonal and diurnal curves of  $g_s$  values, VPD and LAI data,  $E_A$  was esti-  
 235 mated for  $S_{dry}$  and  $S_{wet}$  stands. Estimation also involved the calculation of the decou-  
 236 pling coefficient ( $\Omega$ ) of Jarvis and McNaughton (1986), which is a measure of the  
 237 coupling between conditions at the canopy surface and in the free air stream. For  
 238 the study stands and days, we have estimated  $\Omega$  values moderately high (0,34 on  
 239 average), as a result of large stomata and low wind velocities. This value indicated  
 240 a rather low stomata control of transpiration (which grows progressively weaker as  
 241  $\Omega$  approaches 1.0) if compared with other broadleaf forests (Jarvis and McNaughton  
 242 1986; Goldberg and Bernhofer 2008).

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

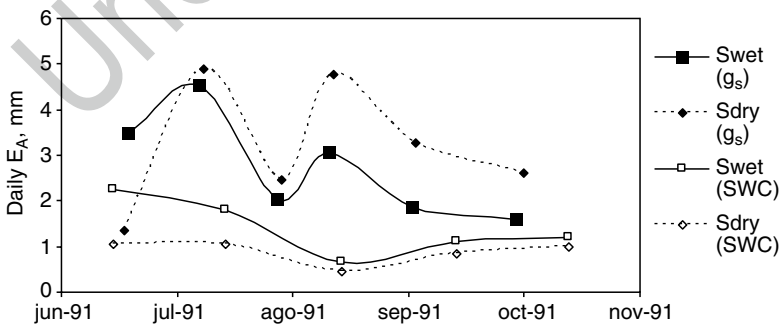


Fig. 10.5 Mean values of daily actual evapotranspiration ( $E_A$ ) in two (dry and wet sites) estimated from stomata conductance ( $g_s$ ) and from time course of soil water content (SWC)

## Lessons Learn 252

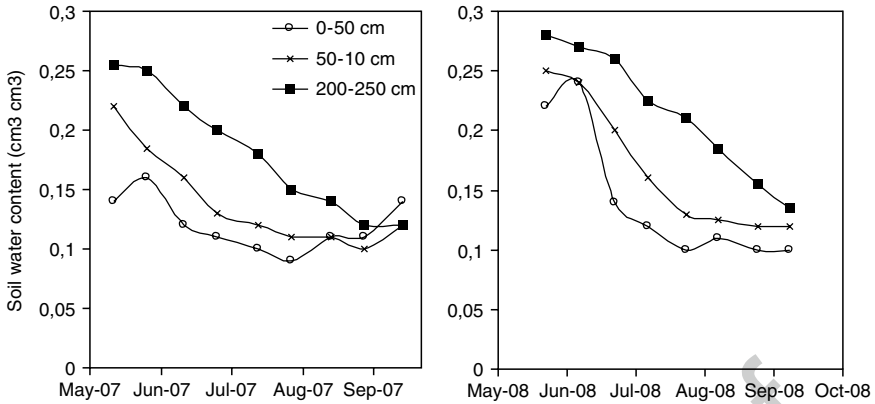
### ***Quercus pyrenaica* Oak Is Only Slightly Water-Limited During Summer Drought** 253 254

In response to progressive decreases in soil water, no substantial changes were found in  $\Psi_1$  or in  $g_s$ , with a tendency to use up water reserves from progressively deeper soil layers, thereby avoiding marked stomata closure. *Q. pyrenaica* seems well adapted to surviving summer drought period while maintaining photosynthetic activity and it seems to have a non-conservative strategy of water consumption (sense Jones 1992), according to patterns described by other authors for different deciduous oaks (Mediavilla and Escudero 2003; Manes et al. 2006).  $\Psi_1$  and  $g_s$  of *Q. pyrenaica* remained high when SWR had been completely depleted. Tree transpiration ( $E_A$ ) only decreased slightly during summer in dry and wet stands of 'Sierra de Gata' mountains and other stands of Central–Western Spain (Hernández-Santana et al. 2008b). However, stand  $E_A$  estimated from the soil water balance gave values much lower than those estimated from the leaf conductance, in spite of the fact that the latter only included tree transpiration and the former included soil evaporation (presumably negligible) and understorey (shrubs and grasses) transpiration, besides the tree transpiration. Irrespective of possible imprecision on  $E_A$  estimates, differences among both approaches allow speculating that trees take up water from an extra water reserve.

### ***Quercus pyrenaica* Oaks Depend on Thick Porous-Weathered Bedrocks** 272 273

The ability to take up water stored in the upper few meters of the weathered bedrock during the pronounced dry season is likely the key feature allowing *Q. pyrenaica* to thrive under dry summer conditions in the shallow, rocky soils of study sites, as other authors have shown for other Mediterranean-type ecosystems (Sternberg et al. 1996; Witty et al. 2003; Schiller et al. 2007). Although weathered bedrock has much lower available-water capacities in the four *Q. pyrenaica* stands than those of soils (Table 10.1), the weathered rock zone is much thicker (several meters) than the soil (< –1 m). From our data, we estimated that a hydraulically active bedrock of around –2.2 and –4.8 m depth (on schist and granite soils, respectively, derived of old weathering during the last interglacial periods; Gallardo and Molina 1979) can provide the water needed by *Q. pyrenaica* trees during summer in the study area. Witty et al. (2003) reported that weathered bedrock supplied at least 70% of the water used by the *Pinus jeffreyi* during the growing season in Sierra Nevada mountains, USA.

The scarce information available on the *Quercus pyrenaica* rooting system indicates a rapid decrease of root length density with depth (Schneider et al. 2001) and also



**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)

289 that most of the root is located in the first –50 cm of the soil (Hernández-Santana  
 290 et al. 2008a). However, deep rooting has been suggested to be a key trait to over-  
 291 come water depletion in the upper soil layers during the dry season in Mediterranean  
 292 ecosystems (Rambal 1984; David et al. 2004; Kurz-Besson et al. 2006; Querejeta  
 293 et al. 2007). Indeed, Cubera and Moreno (2007) and Hernández-Santana et al.  
 294 (2008b) have shown that *Q. ilex* and *Q. pyrenaica* stands of Central–Western Spain  
 295 use soil water located deeper than –2.5 m depth (Fig. 10.6).

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

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

308 Morphological (e.g., low LAI) and physiological (e.g., low  $\Psi_{tp}$  and  $\pi_o$ , and high  
 309  $\epsilon_{max}$ ) differences between *Q. pyrenaica* and other deciduous oaks will be surely  
 310 crucial under this global change scenario.  $E_A$  values here reported and those  
 311 reported by Hernández-Santana et al. (2008a) for *Q. pyrenaica* can be qualified as  
 312 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  $\Psi_1$ . 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, Hincley 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

- 359 Cubera E, Moreno G (2007) Effect of single *Quercus ilex* trees upon spatial and seasonal changes  
360 in soil water content in Dehesas of central western Spain. *Ann For Sci* 64:355–364
- 361 Damesin C, Rambal S, Joffre R (1998) Cooccurrence of trees with different leaf habit: a functional  
362 approach on Mediterranean oaks. *Acta Oecol* 18:195–204
- 363 Davi H, Barbaroux C, Francois C, Dufrière E (2009) The fundamental role of reserves and hydraulic  
364 constraints in predicting LAI and carbon allocation in forests. *Agr For Meteorol* 149:349–361
- 365 David TS, Ferreira MI, Cohen S, Pereira JS, David JS (2004) Constraints on transpiration from an  
366 evergreen oak tree in southern Portugal. *Agric For Meteorol* 122:193–205
- 367 Duhme F, Hinckley TM (1992) Daily and seasonal variation in water relations of macchia shrubs  
368 and trees in France (Montpellier) and Turkey (Antalya). *Vegetatio* 99–100:185–198
- 369 Gallardo JF (2000) Biogeochemistry of Mediterranean forest ecosystems: a case study. In: Bollag  
370 JM, Stotzky G (eds) *Soil biochemistry*. Marcel Dekker, New York, pp 423–460
- 371 Gallardo JF, Martín A, Santa-Regina I (1998) Nutrient cycling in deciduous forest ecosystems of  
372 the ‘*Sierra de Gata*’ mountains: aboveground litter production and potential nutrient return.  
373 *Ann Sci For* 55:749–769
- 374 Gallardo JF, Molina E (1979) Relaciones entre procesos edáficos y superficies morfológicas de la  
375 Cuenca Duero, vol 1, *Actas I Reunión Geológica*. Salamanca, Spain, pp 211–223
- 376 Gallego HA, Rico M, Moreno G, Santa Regina I (1994) Leaf water potential and stomatal  
377 conductance in *Quercus pyrenaica* Willd forests: vertical gradients and response to environ-  
378 mental factors. *Tree Physiol* 14:1039–1047
- 379 Goldberg V, Bernhofer C (2008) Testing different decoupling coefficients with measurements and  
380 models of contrasting canopies and soil water conditions. *Ann Geophys* 26:1977–1992
- 381 Grier CC, Running SW (1977) Leaf area of mature northwestern coniferous forests: relation to the  
382 site water balance. *Ecology* 58:893–899
- 383 Hernández-Santana V, David TS, Martínez-Fernández J (2008a) Environmental and plant-based  
384 controls of water use in a Mediterranean oak stand. *For Ecol Manag* 255:3707–3715
- 385 Hernández-Santana V, Martínez-Fernández J, Morán C, Cano A (2008b) Response of *Quercus pyre-*  
386 *naica* (melojo oak) to soil water deficit: a case study in Spain. *Eur J For Res* 127:369–378
- 387 IPCC (2007) *Climate change 2007: the physical scientific basis*. Cambridge University Press,  
388 Cambridge, UK, 1009 pp
- 389 ISSS-ISRIC-FAO 1998. *World Reference Base for Soil Resources*. World Soil Resources, Reports  
390 No. 84. FAO UN, Rome, 1998
- 391 Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to  
392 region. *Adv Ecol Res* 15:1–49
- 393 Jones HG (1992) *Plants and microclimate. A quantitative approach to environmental plant physi-*  
394 *ology*. Cambridge University Press, Cambridge
- 395 Kurz-Besson C, Otieno D, Lobo do Vale R, Siegwolf R, Schmidt M, Herd A, Nogueira C, David T,  
396 David J, Tenhunen J, Pereira J, Chaves M (2006) Hydraulic lift in cork oak trees in a savannah-  
397 type Mediterranean ecosystem and its contribution to the local water balance. *Plant Soil*  
398 282:361–378
- 399 Llorens P, Domingo F (2007) Rainfall partitioning by vegetation under Mediterranean conditions.  
400 A review of studies in Europe. *J Hydrol* 335:37–54
- 401 Manes F, Vitale M, Donato E, Giannini M, Puppi G (2006) Different ability of three Mediterranean  
402 oak species to tolerate progressive water stress. *Photosynthetica* 44:387–393
- 403 Martínez-Vilalta J, Piñol J, Beven K (2002) A hydraulic model to predict drought-induced mortality in  
404 woody plants: an application to climate change in the Mediterranean. *Ecol Model* 155:127–147
- 405 Mediavilla S, Escudero A (2003) Stomata l responses to drought at a Mediterranean site: a compara-  
406 tive study of co-occurring woody species differing in leaf longevity. *Tree Physiol* 23:987–996
- 407 Merino J, Field C, Mooney HA (1982) Construction and maintenance costs of Mediterranean-climate  
408 evergreen and deciduous leaves. I. Growth and CO<sub>2</sub> exchange analysis. *Oecologia* 53:208–213
- 409 Moreno G, Gallardo JF, Ingelmo F, Cuadrado S, Hernández J (1996) Soil water budget in 4  
410 *Quercus pyrenaica* forests across a rainfall gradient. *Arid Soil Res Rehabil* 10:65–84
- 411 Moreno G, Obrador JJ, Cubera E, Dupraz C (2005) Root distribution in dehesas of Central-  
412 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* 31:168–173 413  
414

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biol* 9:131–140 415  
416

Peñuelas J, Lloret F, Montoya R (2001) Severe drought effects on Mediterranean woody flora in Spain. *For Sci* 47:214–218 417  
418

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* 39:409–417 419  
420  
421

Rambal S (1984) Water balance and pattern of root water uptake by a *Quercus coccifera* L. evergreen scrub. *Oecologia* 62:18–25 422  
423

Rambal S (1993) The differential role of mechanisms for drought resistance in a Mediterranean evergreen shrub: a simulation approach. *Plant Cell Environ* 16:35–44 424  
425

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* 53:221–234 426  
427  
428

Rodá F, Retana J, Gracia CA, Bellot J (1999) Ecology of Mediterranean evergreen oak forests. Springer, Berlin, p 373 429  
430

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 135–144 431  
432  
433

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* 238:147–155 434  
435  
436

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* 34:151–155 437  
438  
439

Silla F, Escudero A (2006) Coupling N cycling and N productivity in relation to seasonal stress in *Quercus pyrenaica* Willd. samplings. *Plant Soil* 282:301–311 440  
441

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* 68:413–416 442  
443  
444

Sternberg PD, Anderson MA, Graham RC, Beyers JL, Tice KR (1996) Root distribution and seasonal water status in weathered granitic bedrock under chaparral. *Geoderma* 72:89–98 445  
446

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 65–112 447  
448  
449

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* 60:185–193 450  
451  
452

Winkel T, Rambal S (1990) Stomata l conductance of some grapevines growing in the field under a Mediterranean environment. *Agric For Meteorol* 51:107–121 453  
454

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* 114:389–400 455  
456



# 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