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Daily sap flow rate as an indicator of drought avoidance mechanisms in five Mediterranean perennial species in semi-arid southeastern Spain

Esteban Chirino · Juan Bellot · Juan R. Sánchez

Abstract Daily sap flow rate was determined in five Mediterranean species (*Pinus halepensis, Quercus coccifera, Pistacia lentiscus, Erica multiflora,* and *Stipa tenacissima*) under two slope aspects (north- and south-facing) in a semi-arid area (Alicante, SE Spain). Sap flow velocity was measured in January, May, August and October of two consecutive years (1998 and 1999) using the stem heat balance (SHB) method. Our results have demonstrated the effects of global radiation (R_g), vapour pressure deficit (VPD) on the sap flow velocity per unit of leaf area. Mean daily sap flow rates (Q_{md}) showed values between 0.001 and 0.202 g H_2O cm^{-2} leaf area day^{-1}. Q_{md} values were higher on the south-facing slope than on the north-facing slope. In most species, the Q_{md} was higher in 1998 than in 1999 due to the higher soil water content, temperature and VPD in 1998. In all five species, a decrease in predawn leaf water potential was accompanied by a decrease in mean daily sap flow rates; nevertheless, the responses of the five species to water deficit conditions were different. In this context, we have linked the drought avoidance mechanisms of the different species through the combined use of daily sap flow rate and predawn leaf water potential under different water deficit conditions. We conclude that *Pinus halepensis, Pistacia lentiscus* and *Erica multiflora* show

water-savers mechanisms to cope with drought, while *Quercus coccifera* and *Stipa tenacissima* show water-spenders mechanisms.

Keywords Drought resistance mechanisms · Water saver · Water spender · Transpiration · Ecophysiology

Introduction

Dry and semiarid ecosystems in the Mediterranean region are characterized by summers with long water deficit periods and high values of global radiation, temperature and vapour pressure deficit (Di Castri 1973). These environmental conditions affect the physiological activity of plants (Larcher 1995; Gazal et al. 2006) producing changes in plant water consumption through stomatal regulation (Salleo et al. 2000; Mediavilla and Escudero 2004) which, in turn, influence the sap flow rate (Badalotti et al. 2000; David et al. 2007; Gartner et al. 2009).

On drought stress conditions, the species have developed adaptations for escaping or resisting to drought. Drought resistance can be by means of two strategies: drought avoiding or drought tolerating. There is two distinct kinds of drought avoidance mechanisms: (1) water saver, that avoid drought by water conservation, and (2) the water spender, that avoid drought by absorbing water sufficiently rapidly to keep up with their extremely rapid water loss. These concepts and definitions exposed by Levitt (1980) have been applied in several studies with the aim of assess the drought resistance strategy of species. In this sense, previous papers have assessed some species of the present study. *Pinus halepensis, Erica multiflora* and *Pistacia lentiscus* have been assessed as drought avoidance

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species (Vilagrosa 2002; Ferrio et al. 2003; Lorens et al. 2003b; Baquedano and Castillo 2007); while *Quercus coccifera* has been assessed as a drought-tolerant species (Martínez-Ferri et al. 2000; Baquedano and Castillo 2006).

In semiarid areas of the Mediterranean Spain, some changes in the reforestation strategy have been observed in the last decades. In several cases, has been prioritized the introduction of native shrubs and grasses, unlike of extensive conifer reforestation (e.g. Aleppo pine) carried out during the second part of the twentieth century. In this context, knowledge about plants strategies to cope with drought, as well as the drought avoidance mechanisms of the species introduced acquires great importance; because would allow to link the selection of species for forest restoration with the soil water availability on the plantation site and the water demand of the species (Vilagrosa et al. 2003a; Vallejo and Alloza 2004).

Taking all the above into consideration, in this paper, we analyzed the daily sap flow rates in one tree species (*Pinus halepensis*), three shrub species (*Quercus coccifera, Pistacia lentiscus and Erica multiflora*), and an *alpha* grass steppe (*Stipa tenacissima*) in a semiarid ecosystem, under two slope aspects (north- and south-facing). The hypotheses of this work were: (1) Sap flow rate is affected by microclimatic conditions and soil water availability, therefore hopefully observe: (a) a common seasonal pattern in the sap flow rate by species, (b) higher sap flow rate in south-facing than north-facing slope, and (c) higher sap flow rate during the wetter year; and (2) Sap flow response of plants to cope with water deficit stress, expressed by means of predawn water potential, can be linked with drought avoidance mechanisms (water saving or water spending). To test these hypotheses, the aims of this paper were (1) evaluate the effect of microclimatic conditions and soil water content on the sap flow rate by species in the time (seasonal pattern and year) and slope aspect; and (2) establish a link between the daily sap flow of the different species as response to variations in predawn leaf water potential and drought avoidance mechanisms of plants (water saver or water spender).

Materials and methods

Site description

The research was carried out at the "El Ventós" experimental station, Alicante, Spain. Altitude 600 m asl and slopes between 23° and 26°. Loam and loamy limestone support calcareous Cambisol and Lythic Leptosol (FAO-UNESCO), with average soil depth of 20 cm, organic matter content of 4.7%, clay content between 48 and 58%, total porosity of 50.2%, field capacity of 25% and average

infiltration rates measured with a double-ring infiltrometer were between 192 and 438 mm h^{-1} (Bellot et al. 2001; Chirino et al. 2006). The climate is semi-arid Mediterranean, with a very high inter-annual variability. Mean annual temperature is 18.2°C and mean annual rainfall is 275 mm (1976–2006 period). The current vegetation landscape in the study area is composed of different land cover types (patch-mosaic) which can be situated along a successional gradient of increasing structural complexity of vegetation: degraded open land or bare soil, sometimes occupied by microphytic crusts (Maestre et al. 2002); dry grassland formations of *Brachypodium retusum* Pers. Beauv., with dwarf scrubs (*Anthyllis cytisoides* L., *Helianthemum syriacum* (Jacq.) Dum.-Cours. and *Thymus vulgaris* L.); and more mature landscape patches composed of scattered thorn and sclerophyllous shrublands with *Quercus coccifera* L., *Pistacia lentiscus* L., *Erica multiflora* L., *Rhamnus lycioides* L. and *Rosmarinus officinalis* L. (Bonet et al. 2001). Other anthropogenic components of the present landscape mosaic are afforestations with *Pinus halepensis* Mill. on dry grasslands and thorn shrublands. On south-facing slopes, the predominant vegetation is a rather interspersed mosaic of open *Stipa tenacissima* steppes and dwarf shrubland with gradual transitions between them (Bautista et al. 2007). A description of the land cover types has been presented by Chirino et al. (2006).

Experimental design for sap flow measurements and data processing

Sap flow rate measurements were carried out in sets of five consecutive days during the months of January (winter), May (spring), August (summer) and October (autumn) in the years 1998 and 1999. These measurements were taken in four species on a north-facing slope (*Pinus halepensis* Mill., *Quercus coccifera* L., *Pistacia lentiscus* L. and *Erica multiflora* L.) and four species on a south-facing slope (*Pinus halepensis* Mill., *Quercus coccifera* L., *Pistacia lentiscus* L. and *Stipa tenacissima* L.). On both slopes, Aleppo pines (*Pinus halepensis*) were planted 40 years ago, while the other species belonged to the natural succession. For each slope aspect (north- and south-facing) three individuals were selected randomly by species for the sap flow measurements. The height of the individuals is shown in Table 1. Leaf Area Index (LAI, Table 1) was measured in individuals similar to those where the sap flow was monitored. LAI was measured by means of a destructive method based on the leaf area of the shoot biomass in a rectangular prism with square base of 50 × 50 cm and a height according to the individuals sampled.

To measure the sap flow we used the stem heat balance method (SHB system, van Bavel 1984). In each of the plants selected we installed three sap flow gauges

Table 1 Height of the individuals selected by species for sap flow measurements

Species	Slope	Characteristics of individuals	
		Height (m)	LAI (m^2/ m^{-2})
P. halepensis	North	4.57 ± 0.30	1.11 ± 0.36
	South	1.83 ± 0.12	0.87 ± 0.23
Q. coccifera	North	1.41 ± 0.12	1.01 ± 0.27
	South	0.61 ± 0.05	1.78 ± 0.32
P. lentiscus	North	1.58 ± 0.19	1.96 ± 0.03
	South	0.57 ± 0.07	0.45 ± 0.07
E. multiflora	North	0.85 ± 0.03	0.59 ± 0.04
S. tenacissima	South	0.72 ± 0.07	2.06 ± 0.10

Leaf area index (LAI) of similar individuals used for sap flow measurements (Data May 1997; $N = 3$)

(Dynagauge, Dynamax Inc., Houston, USA, models SGA2, SGA3 or SGA5) on upper third crown on branches oriented in three directions (N, SE, SW). In the case of *P. halepensis,* it was necessary to use a 5 m tall scaffolding to reach the upper third of the plant crown. Moreover, additional insulation and an exterior wrapping of tinfoil were also used to provide higher isolation from meteorological conditions. Measurements of sap flow velocity (Q; g H_2O h^{-1}) were programmed with a scan interval of 1 min and signals were averaged every 15 min. After removing the gauges, the leaf area of each branch was measured destructively to normalize sap flow velocity per unit of leaf area (Q_1; g H_2O cm^{-2} leaf area h^{-1}). Leaves were scanned with a professional scanner (Epson Expression 1680 Pro, Seiko Epson Corporation, Nagano, Japan). The images obtained were analyzed with the specific image processor WinRHIZO software (Regent Inst., Canada) to obtain leaf area (cm^2). FLOW32 software requests a time interval of reduced power, and during this time interval, the flow rate is set to zero (van Bavel, 1984). In our case, we defined the least time possible (power-down time: 00:00 AM and power-up time: 3:00 AM). Thus, the daily sap flow rate by individual (Q_d; g H_2O cm^{-2} leaf area day^{-1}) was computed by means of the Q_1 accumulated from 3:00 to 24:00. Mean daily sap flow rate (Q_{md}; g H_2O cm^{-2} leaf area day^{-1}) was computed by averaging the Q_d value obtained from three individuals selected in each sampled periods. Subsequently, we estimated the mean daily sap flow rate for each species by month (January, May, August and October), year (1998 and 1999) and slope aspect (north- and south-facing).

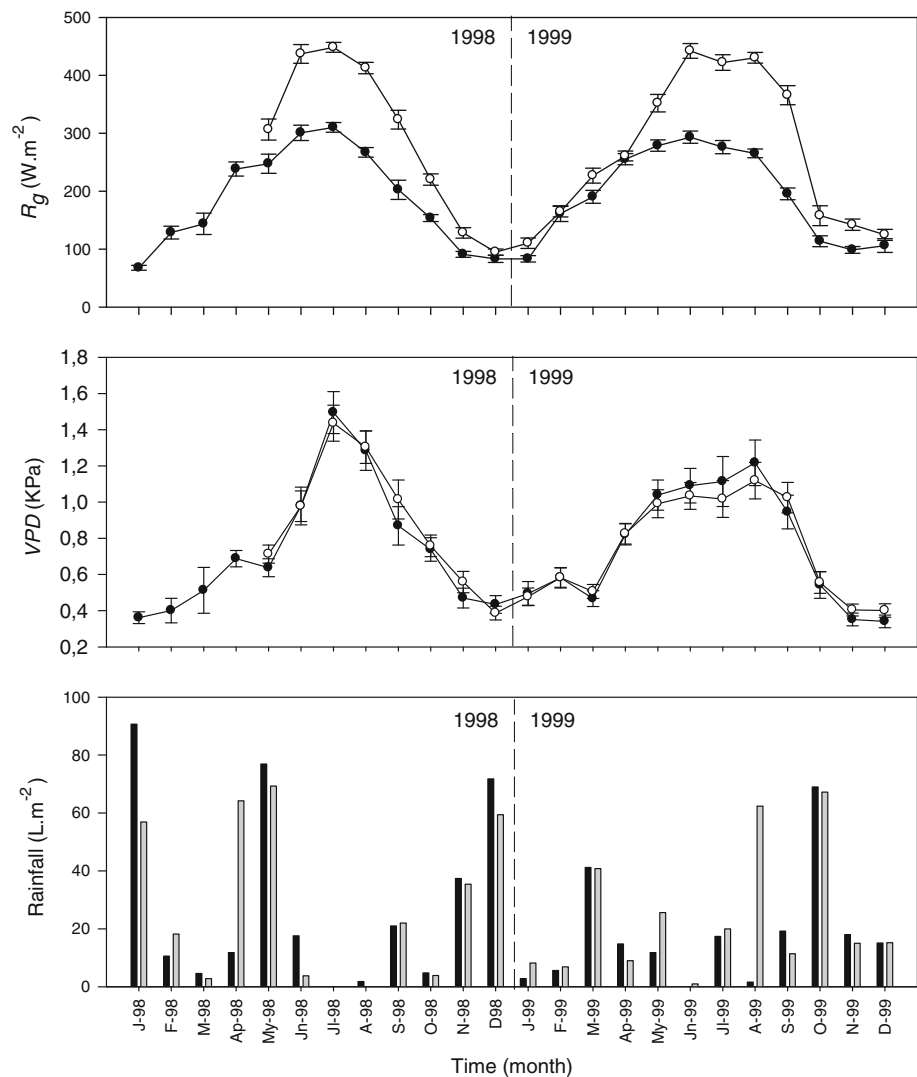Meteorological conditions, soil moisture and predawn water potential

Meteorological data were monitored during 1998 and 1999. Rainfall, air temperature (T^a), air humidity (H) and global radiation (R_g) were measured continuously with an automatic weather station Campbell Scientific CR10 (Campbell Scientific Ltd. UK). The automatic weather station on north-facing slope was installed since 1995, while on the south-facing slope was installed in March, 1998. T^a, H and R_g were taken at 10 min intervals and averaged every hour. Vapour pressure deficit (VPD) was calculated from T^a and H data. Soil moisture was monitored using the Time Domain Reflectometry System (Reflectometer Tektronic 1502C, Metallic TDR cable Tester, Tektronix, Beaverton, OR, USA) from 0 to 30 cm (maximum soil depth) by means of 12 probes inserted in a patch-mosaic of three vegetation cover types: pine with dry grass and sclerophyllous shrub on the north-facing slopes and *alpha* grass steppes of *S. tenacissima* on the south-facing slopes (Chirino 2003). Relative Extractable Water (REW) in the root zone was calculated from the soil moisture monitored in these vegetation types by means of the equation REW = $(\theta - \theta_{mín})/(\theta_{FC} - \theta_{mín})$ described by Granier (1987) and Bréda et al. (1995), where θ is the actual soil water content and $\theta_{mín}$ is the minimum soil water content observed during the soil moisture monitoring, and $\theta_{FC} = \theta$ at field capacity. All the variables are expressed in L m^{-2}. REW = 0.4 was identified as the threshold for soil water deficit (Granier 1987; Bréda et al. 1995). Leaf water potential before sunrise (predawn leaf water potential: Ψ_{pd}) was measured by using the Scholander pressure chamber (Soil moisture Equipment Corp., Santa Barbara, CA, USA) in three branches of three individuals selected by species. This variable was measured in all species, except in *Stipa tenacissima* due to technical difficulties.

Statistical analysis

Statistical analysis was carried out with the STATISTICA 6.0 package (Statsoft Inc., Tulsa, USA). Means monthly Q_{md} were compared using a General lineal Model (GLM) Repeated Measures by means of multi-way within-subject designs. We used the years (1998 and 1999) and monthly Q_{md} value as within-subjects factors, and slope aspect and species as between-subjects factors. Due to interactions observed in the results of GLM Repeated Measures (multi-way within-subject designs), subsequently was carried out a GLM Repeated Measures with one within-subject factor (monthly Q_{md}) and only a between-subject factor (slope aspect, year or species). In the case of species analysis, a *post hoc Tukey HSD* was used. In order to know the differences or patterns commons between monthly Q_{md} of species, a two-factor Univariate ANOVA (year and month) was carried out, using a *post hoc Tukey HSD*. Meteorological data on the annual periods (full data on north-facing slope) were compared by means of analysis of variance (one way ANOVA). Data on T^a (°C), H (%), R_g (W m^{-2}), VPD (kPa) and rainfall by month and slope aspect were compared using nonparametric statistical methods (Mann–Whitney test and "t" test)

Fig. 1 Comparison between north- and south-facing slopes with respect to global radiation (R_g), vapour pressure deficit (VPD) and rainfall during 1998 and 1999. Data on R_g and VPD are mean monthly ± standard error (north-facing: *black circle* and *solid line*; south-facing: *white circle* and *solid line*). Rainfall data are monthly accumulated values (north-facing: *black bar*; south-facing: *grey bar*)

due to differences in the number of observations. The north-facing slope had full data for the years 1998 and 1999; in contrast, the south-facing slope had data only from March, 1998 to December, 1999, when the automatic weather station was installed. The relationship between Q_{md} (g H_2O cm^{-2} day^{-1}) and Ψ_{pd} (MPa) in each species was calculated by means of a exponential regression. In the case of the relationship between Q_1 (g H_2O cm^{-2} h^{-1}) and the hourly value of R_g (W m^{-2}) and VPD (kPa) throughout the day we used exponential, quadratic and linear regressions.
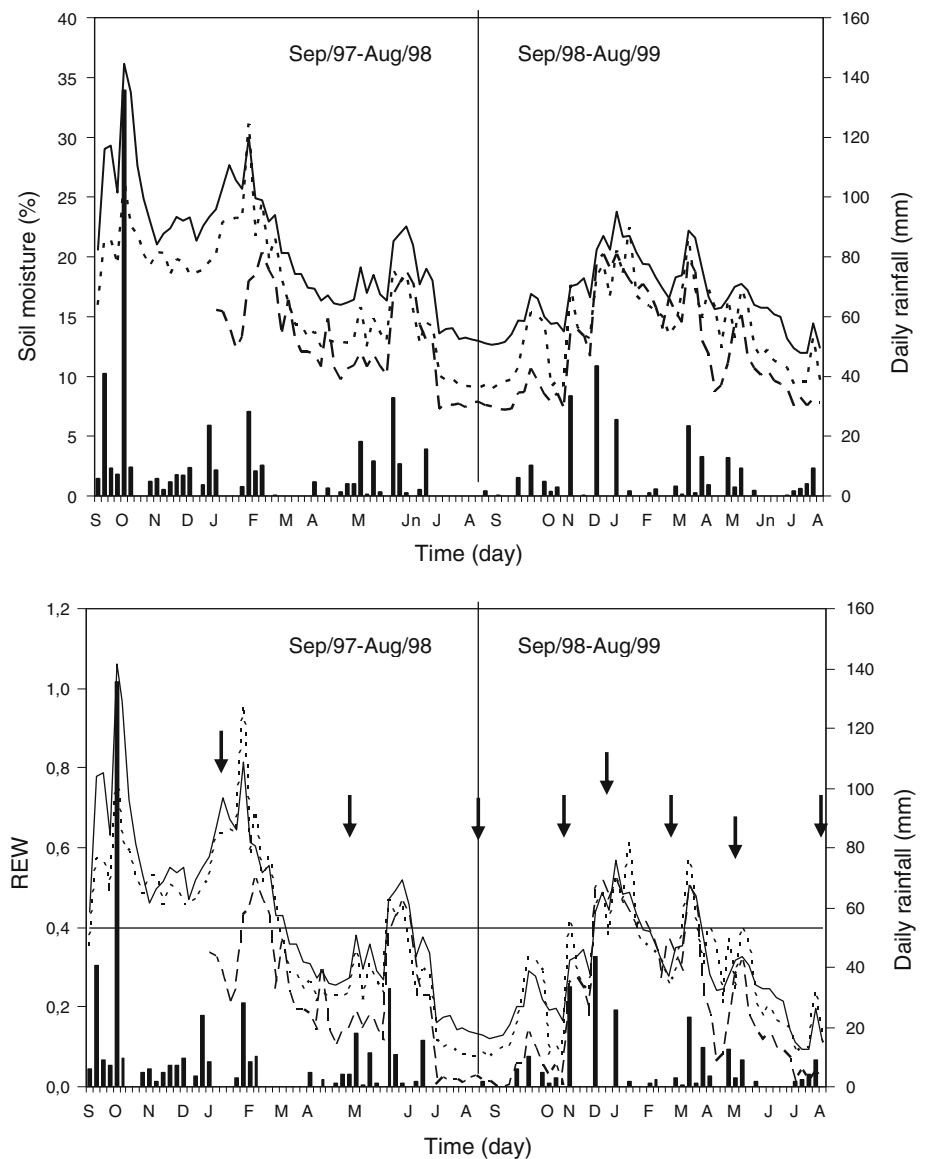
Results

Meteorological variables and soil moisture

Monthly global radiation (R_g) was higher on the south-facing slope than on the north-facing slope (Fig. 1; $p < 0.001$). No

significant differences between slope aspects were found with respect to rainfall and VPD (Fig. 1). Nevertheless, both slope aspects showed significant differences ($p < 0.001$) between measuring months for the variables T^a, R_g, and VPD. On an annual time scale, T^a ($p = 0.028$) and VPD ($p = 0.011$) were higher in 1998 than in 1999. Annual rainfall was 1.2 times higher in 1998 (288.3 mm) than in 1999 (241.1 mm), resulting in higher soil moisture values and REW during the first year (Fig. 2). Soil moisture average on north-facing slope ranged between 18.1% in pine with dry grass and 15.2% in sclerophyllous shrub; while, on south-facing slope represented by alpha grass steppe of *S. tenacissima* the soil moisture average was 12.7% (Fig. 2, above). REW values on both slope aspects were below the threshold established for Mediterranean vegetation cover (REW = 0.4), which in our case represents a soil water content of 40% below field capacity (Fig. 2, below). These results point to the long duration of soil water deficit conditions in the study area.

Fig. 2 Daily rainfall and soil moisture (above), and Relative Extractable Water (REW, below) in two hydrological years 1997/1998 and 1998/1999. The data showed in the x-axis correspond to daily measurements. We show label of months to improve the understanding. On north-facing slope: pine with dry grass (*solid line*) and sclerophyllous shrub (*dashed line*). On south-facing slope: alpha grass steppes of *S. tenacissima* (*long dash*). REW = 0.4 is threshold for Mediterranean species (*dotted line*). Months of sap flow measurements: *vertical arrow*
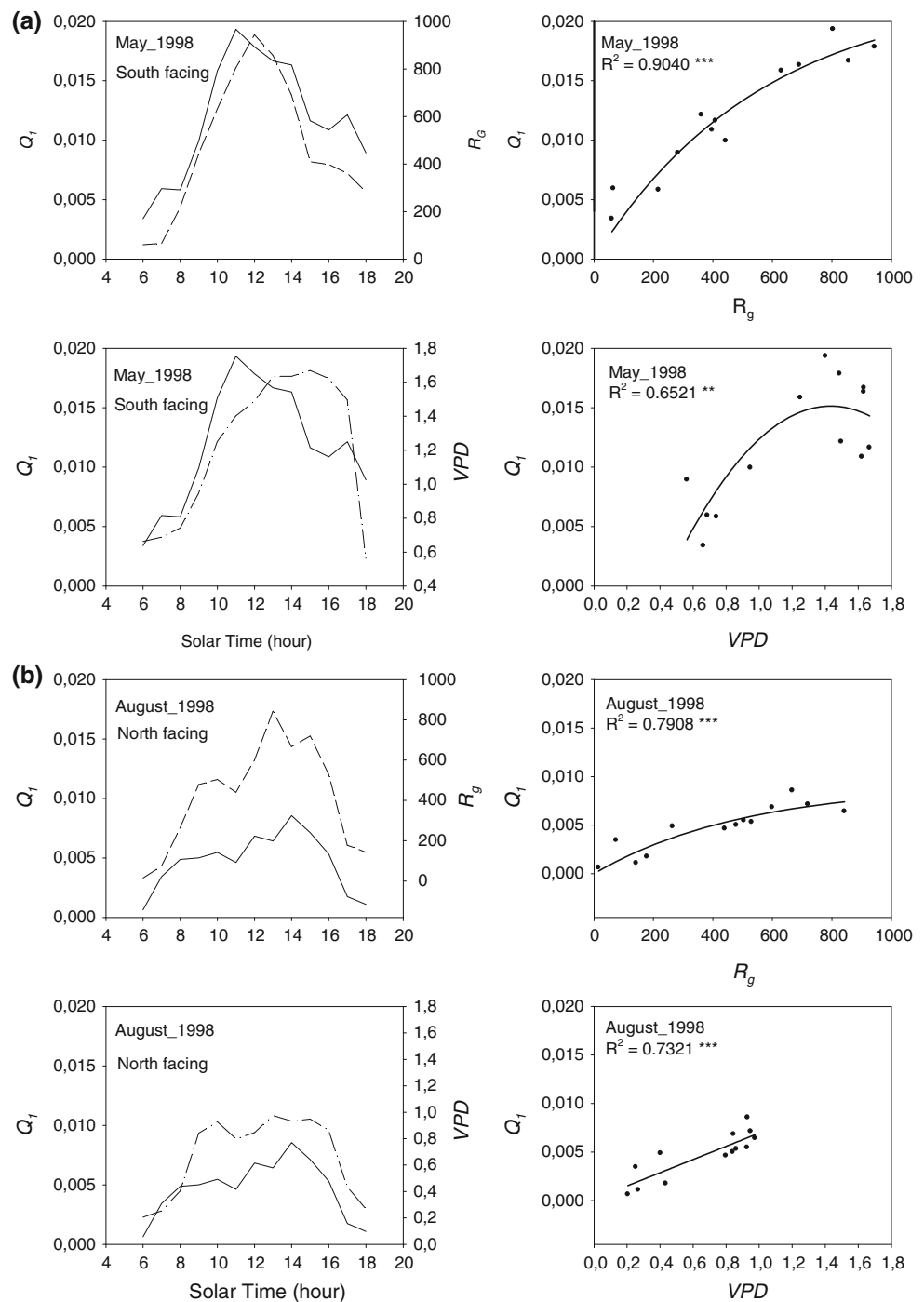

Only from September, 1997 to March, 1998 were the REW values higher than the threshold, as a result of the extraordinary rains in the autumn of 1997.

Relationship between sap flow and meteorological variables

During the course of the day, the sap flow velocity per unit of leaf area (Q_1) showed a significant relationship with R_g and VPD. As an example, we present the results obtained for *Quercus coccifera* on two different dates in 1998, with contrasting soil moisture and meteorological conditions. The first case (Fig. 3a) shows the results of the May 28th sap flow measured on the south-facing slope, with high daily soil water content (19.8%) and high daily VPD (1.22 kPa).

The second case (Fig. 3b) shows the August 19th sap flow measured in north-facing conditions, with a lower daily soil water content (10.3%) and lower daily VPD (0.67 kPa). In both cases, R_g presents a significant relationship with Q_1, by means of an exponential equation $\left[Q_1 = a*\left(1 - e^{-b*R_g}\right)\right]$ where extreme values of R_g tend to produce Q_1 approaching the asymptote. VPD shows a quadratic polynomial equation $\left[Q_1 = a + b_{0*}\,\text{VPD} + b_{1*}\,\text{VPD}^2\right]$ on May 28th and a linear equation $\left[Q_1 = a + b_{0*}\,\text{VPD}\right]$ on August 19th. These differences in the regression equations are explained by the fact that the first case presented higher values of soil water content and VPD than the second case, which favoured higher Q_1 values. However, when VPD > 1.4 kPa, Q_1 decreased. Similar results were observed in the other species (data no shown).

Fig. 3 Left side shows the hourly variation in sap flow velocity (Q_1: g H_2O cm^{-2} h^{-1}), global radiation (R_g: W m^{-2}) and vapour pressure deficit (VPD: kPa) in *Q. coccifera* (*solid line* Q_1, *short dash* R_g, *dash-dot* VPD. **a** South-facing data: May 28, 1998. **b** North-facing data: August 19, 1998. *Right side* shows the regression equations according to the variables on the left side of the figure (significance differences **$p < 0.01$ and ***$p < 0.001$)

Daily sap flow rate of each species by slope aspect, year and month

Average daily sap flow rates (Q_{md}) of the different species by months and slope aspects during 2 years, 1998 and 1999 (Fig. 4) showed values between 0.001 and 0.202 g H_2O cm^{-2} leaf area day^{-1}. General lineal Model (GLM) Repeated Measures by means of multi-way within-subject designs indicated significant differences ($p < 0.05$) in Q_{md} values between the factors: years, slope aspect and species (Table 2). In this analysis were observed interactions between all factors. Subsequent analysis using GLM Repeated Measures with only a within-subject and between-subject factor determined the effect of each factor (Table 3). *Q. coccifera* and *P. lentiscus* showed higher Q_{md} values on the south-facing slope than on the north-facing slope during
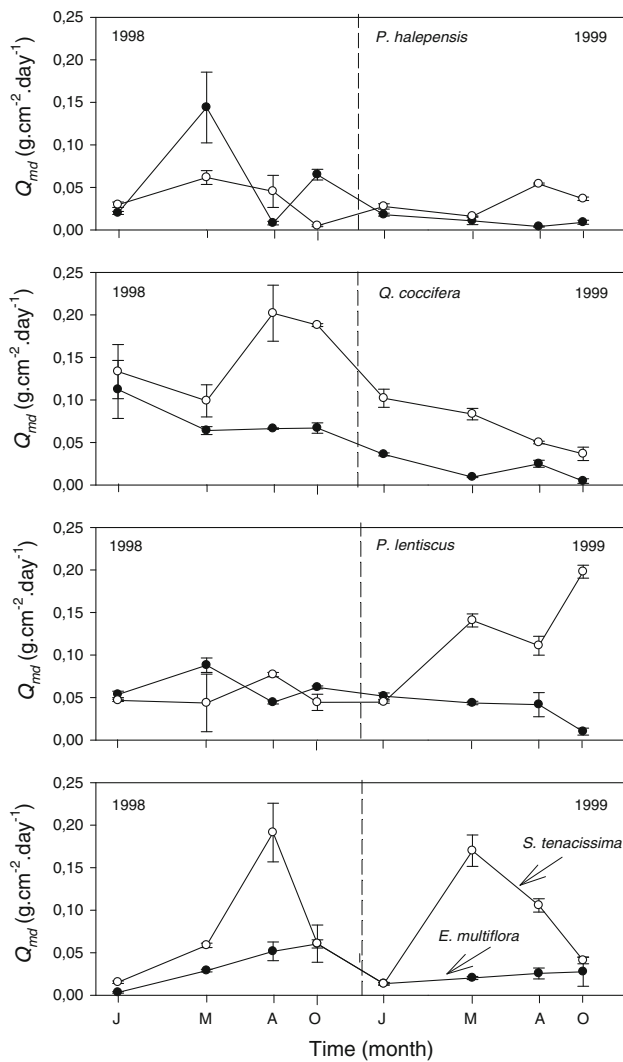
Fig. 4 Monthly sap flow rate by species in each slope aspect (north- and south-facing) and during two years (1998 and 1999). Mean ± standard error, north-facing: *black circle* and *solid line*; south-facing: *white circle* and *solid line*. See in the last figure we show two species, *E. multiflora* from north-facing (*black circle* and *solid line*) and *S. tenacissima* from south-facing (*white circle* and *solid line*)

Table 2 Results of General lineal Model (GLM) Repeated measures by means of multi-way within-subject designs

Factor	F value	p value
Slope aspect	25,580	0.000***
Species	8,880	0.000***
Year	8,380	0.010*
Year * Slope aspect	8,020	0.011*
Year * Species	9,170	0.000***
Month	13,690	0.000***
Month * Slope aspect	6,000	0.001**
Month * Species	7,400	0.000***
Year * Month	3,360	0.025*
Year * Month * Slope aspect	6,110	0.001**
Year * Month * Species	4,500	0.000***

Significance differences * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$

1999 for *P. halepensis*, *P. lentiscus* and *E. multiflora* (Table 3, Time factor $p < 0.05$). Only, were observed interactions between time and years in *P. halepensis* and *P. lentiscus*. On south-facing slope *S. tenacissima* showed higher Q_{md} in 1998, while an opposite result was observed in *P. lentiscus* (Table 3, Time factor $p < 0.05$) showing Q_{md} higher in 1999 than in 1998. *P. halepensis* (on south-facing) and *Q. coccifera* (in both slope aspect) no showed significance differences in the time (Table 3, Time factor $p > 0.05$). Several interactions were observed (Table 3, time × year factor, $p < 0.05$). The year factor (test of between-subjects effects) ratified the results of previous analysis, and indicated significance differences in the annual Q_{md} in *Q. coccifera*.

Comparative analysis of Q_{md} values between species within each slope aspect indicated significant differences (Table 3, Time factor, $p < 0.001$). On the north-facing slope *Q. coccifera* and *P. lentiscus* showed higher Q_{md} than *E. multiflora*; while *P. halepensis* presented an intermediate result, no showing significance differences with the others species. On the south-facing slope *Q. coccifera* showed higher Q_{md} than *S. tenacissima* and *P. lentiscus*. In this slope aspect, *P. halepensis* showed the lowest values (Table 3, Time factor, $p < 0.001$). Both time × species, like the species factor showed interactions and significance differences respectively (Table 3). The analysis of sap flow by species in each slope aspect no showed a common pattern between monthly Q_{md} (Fig. 5). The month of maximum and minimum Q_{md} during the 2 years of measurements was different in each species (Fig. 5). However, on south-facing slope *P. halepensis*, *P. lentiscus* and *S. tenacissima* tended to show the highest Q_{md} values in May and August, and lowest values in January (Fig. 5). On north-facing slope, *P. halepensis* and *P. lentiscus* showed the highest Q_{md} in May and lowest values Q_{md} in August,

period of measurements (Table 3, Time factor $p < 0.05$), while *P. halepensis* showed an opposite result. A higher R_g on south-facing slope could produce stress in *P. halepensis*, induce a stomatal closure and reduce the sap flow. In the cases of *P. halepensis* and *P. lentiscus* were observed interactions between the factors time and slope aspect ($p < 0.05$). The test of between-subjects effects indicated that *Q. coccifera* and *P. lentiscus* presented two times higher Q_{md} in south- than north-facing (Table 3, slope aspect factor $p < 0.01$). *P. halepensis* not showed significance differences.

The inter-annual variability analysis on the north-facing slope indicated that Q_{md} values were higher in 1998 than in

Table 3 Results of General lineal Model (GLM) repeated measures by means of one-way within-subject designs (Greenhouse-Geisser test was used to compare the within-subject effects)

Subjects: Q_{md} values by	Tests of within-subjects effects				Tests of between-subjects effects	
	Time factor		Time × slope aspect		Slope aspect factor	
	F	Sig.	F	Sig.	F	Sig.
Slope aspect factor (north- vs. south-facing)						
P. halepensis	10.889	0.014*	7.448	0.030*	0.004	0.950
Q. coccifera	14.851	0.004**	3.744	0.086	121.902	0.000***
P. lentiscus	6.935	0.027*	24.176	0.001**	101.456	0.001**
	Time factor		Time × year		Year factor	
	F	Sig.	F	Sig.	F	Sig.
Year factor on north-facing						
P. halepensis	8.570	0.041*	8.439	0.042*	21.129	0.010**
Q. coccifera	3.861	0.114	0.641	0.480	55.977	0.002**
P. lentiscus	8.486	0.018*	9.242	0.015*	28.870	0.006**
E multiflora	7.900	0.032*	2.833	0.150	7.793	0.049*
Year factor on south-facing						
P. halepensis	4.405	0.098	7.396	0.048*	0.626	0.473
Q. coccifera	1.094	0.362	6.471	0.053	125.863	0.000***
P. lentiscus	8.780	0.025*	10.571	0.017*	102.803	0.001**
S. tenacissima	23.351	0.003**	10.753	0.015*	0.006	0.942
	Time factor		Time × species		Species factor	
	F	Sig.	F	Sig.	F	Sig.
Species factor within of each slope aspect						
North-facing	17.426	0.000***	6.203	0.000***	8.125	0.008**
South-facing	11.942	0.000***	13.173	0.000***	111.996	0.000***

Significance differences * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$

while *E. multiflora* show the highest and lowest Q_{md} in August and January respectively.
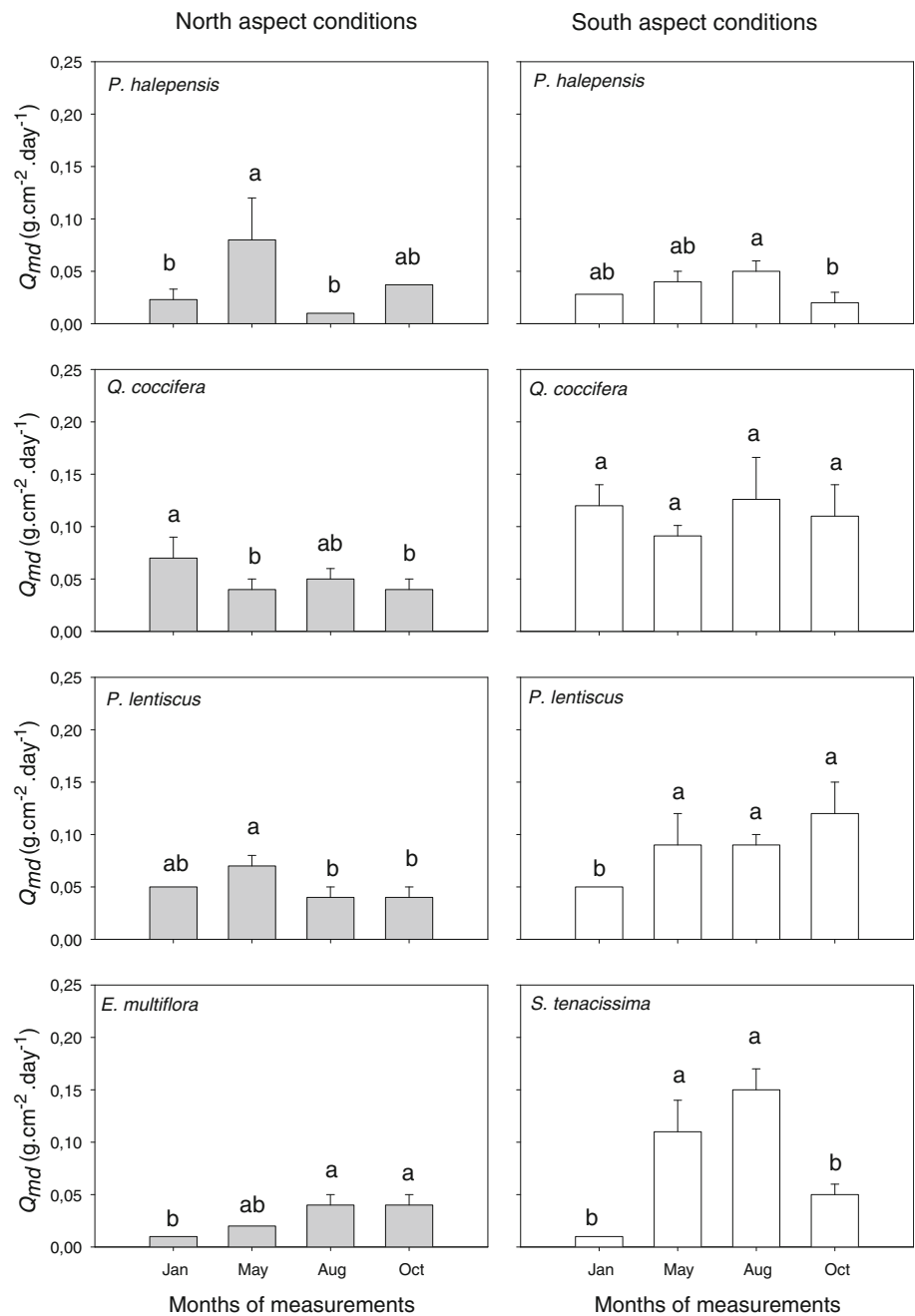
Daily sap flow rate by species under water deficit conditions: drought avoidance mechanisms of species

Predawn leaf water potential (Ψ_{pd}) values during the study period ranged between -0.2 and -3.2 MPa (Fig. 6). With the exception of *P. halepensis*, all the individuals sampled on the south-facing slope showed slightly higher Ψ_{pd} values than those sampled on the north-facing slope, but statistically significant differences were found only in *Q. coccifera* ($p = 0.047$). The relationship between Q_{md} and Ψ_{pd} was verified by means of a exponential regression ($Q_{md} = a*e^{b*\Psi_{pd}}$). The Q_{md} values in each species decreased according to the decrease in Ψ_{pd} (Fig. 6). The slope of the regression equations indicated the different response of the species studied under the different soil water availability conditions present during the monitoring period, expressed by means of predawn leaf water potential. In conditions unaffected by water deficit ($\Psi_{pd} > -1.0$ MPa), *Q. coccifera* showed the highest Q_{md} values, while *P. halepensis* and *P. lentiscus* showed Q_{md} values that were relatively high, but lower than *Q. coccifera*. Under water deficit conditions ($\Psi_{pd} < -2.0$ MPa), both *P. halepensis* and *P. lentiscus* presented decreased Q_{md} values, more notably so in *P. halepensis*. On the other hand, *E. multiflora* showed low Q_{md} values in all conditions as well as a somewhat reduced sap flow with decreases in Ψ_{pd}. It should also be observed that under the lowest Ψ_{pd} (<-2.8 MPa), *Q. coccifera* showed the highest Q_{md} values, which were 36 times higher than the values for *P. halepensis*.

Under different water deficit conditions during the study period, the daily sap flow rate of each species has been

Fig. 5 Average monthly sap flow rate by species in each slope aspect (north- and south-facing). Results of two-factor Univariate ANOVA (*post hoc Tukey HSD*). Sap flow values followed by the same letter are not significantly different at $p < 0.05$
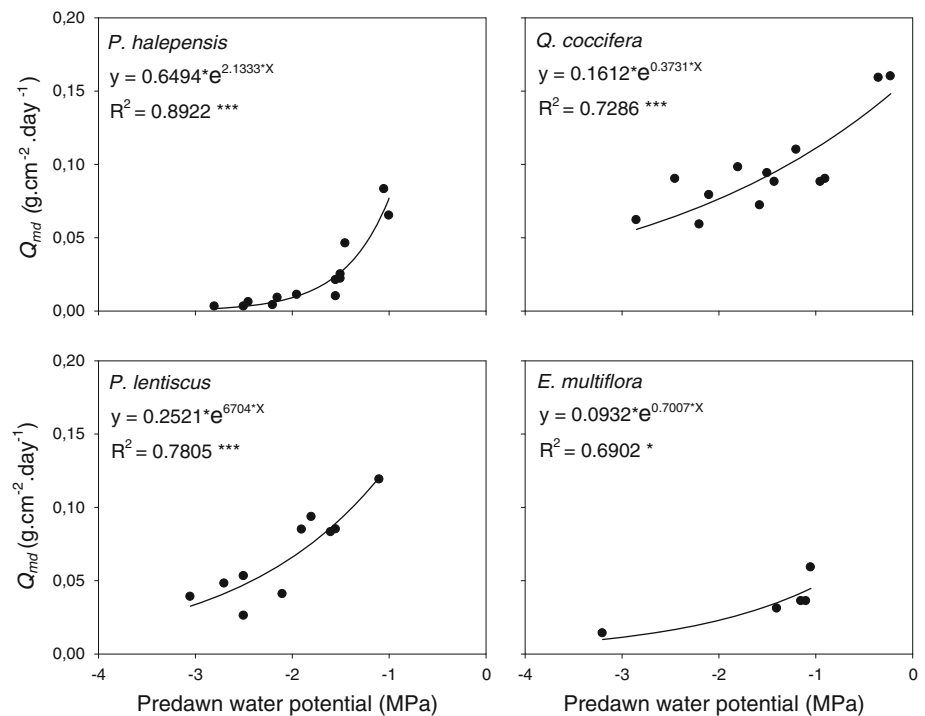

linked with a specific drought avoidance mechanism. In general, all the species studied showed a decrease in Q_{md} values according to the decrease in Ψ_{pd}; nevertheless, the responses of the species to cope with water deficit conditions were different. A species-by-species comparison of the variations in daily sap flow rate with respect to decreases in predawn leaf water potential (Fig. 6), shows that the response of *P. halepensis*, *P. lentiscus* and *E. multiflora* can be linked with water-savers mechanisms. In contrast, *Q. coccifera*'s response can be linked with water-spenders mechanisms.

Discussion

Meteorological variables and sap flow

Results show higher R_g on the south-facing slope than on the north-facing slope (Fig. 1) and a significant relationship between Q_1 and R_g and VPD (Fig. 3), which can explain why most of the individuals studied on the south-facing slope presented a higher Q_{md} values than those on the north-facing slope (Table 3). In this sense, previous works have shown, by means of simple equations or multiplicative

Fig. 6 Relationship between mean daily sap flow rate (Q_{md}) and mean predawn leaf water potential (Ψ_{pd}). Exponential regression equation by species. Data in each measurement period and slope aspect (significance differences $*p < 0.05$, $**p < 0.01$ and $***p < 0.001$)

P. halepensis
$y = 0.6494*e^{2.1333*X}$
$R^2 = 0.8922$ ***

Q. coccifera
$y = 0.1612*e^{0.3731*X}$
$R^2 = 0.7286$ ***

P. lentiscus
$y = 0.2521*e^{6704*X}$
$R^2 = 0.7805$ ***

E. multiflora
$y = 0.0932*e^{0.7007*X}$
$R^2 = 0.6902$ *

models, that sap flow is affected by meteorological variables such as T^a, R_g, PAR, rainfall and other computed variables like VPD (Badalotti et al. 2000; Infante et al. 2003; Moro et al. 2004; Wang et al. 2006; Conejero et al. 2007; Poyatos et al. 2007; Yue et al. 2008; Pfautsch et al. 2010), even at night (Fisher et al. 2007). In fact, some authors have demonstrated that south-oriented branches present higher sap flow rates than north-oriented branches because of higher exposure to radiation (Steinberg et al. 1990). Other previous works have reported a decrease in sap flow rate when VPD is higher than 1.2 kPa (Luis et al. 2005; Poyatos et al. 2008; Dzikiti et al. 2010), as shown in our results (Fig. 3) for sap flow on the south-facing slope.

On the other hand, some studies have also been presented evidences on the relationship between sap flow and weather seasons, based on the interaction between soil water availability, T^a, R_g, VPD and rain distribution; which is observed more easily in regions where clear seasonal differences exist (Farrington et al. 1994). Several species (*Q. ilex, Q. agrifolia, Q. durata, P. latifolia, A. unedo* and *P. australis*) show the maximum sap flow rate in spring or early summer (Goulden 1996; Infante et al. 2003; Martínez-Vilalta et al. 2003; Moro et al. 2004) when the soil water content is optimum and the VPD does not show stress values. Minimum sap flow is linked with low soil water content (e.g. summer), or low VPD, although there is an optimum soil water content as can be observed in winter. In our study, on north-facing slope *P. halepensis* and *P. lentiscus* showed a seasonal pattern similar to previously described; while on south-facing slope these same

species jointly to *S. tenacissima* showed a different seasonal pattern. In general, we do not observe a single seasonal pattern between all species (Fig. 5) as was reported by Martínez-Vilalta et al. (2003); in fact, Luis et al. (2005) also no found a clear seasonal pattern in *P. canariensis*. In our case, we think that although edaphic and meteorological factors impose similar environmental conditions during the measurement period, the species themselves determine the sap flow rate response according to their particular water use strategy, morphology, structural or functional mechanisms to cope with environmental conditions. The species diversity can produce responses diversity.

On an annual time scale, the higher annual rainfall in 1998, preceded by a very wet winter in 97/98 (Fig. 1), contributed to higher soil water content in this year (Fig. 2), which produced that most species in both slope aspect presented a higher sap flow rate in 1998 than in 1999 (Fig. 4). Similar results have been reported by Farrington et al. (1994). The high values of T^a and VPD in 1998, but with lesser value respect to threshold values of stress for these variables, also could contribute to higher the sap flow rate in 1998. In contrast, on south-facing slope is possible that spite the high soil water content, the high T^a and VPD during 1998 were limiting factor of sap flow in some species.

Drought avoidance mechanisms of species

In semiarid ecosystems, water is a limiting resource and plants are often subjected to water deficit conditions (Di Castri 1973; Kramer and Boyer 1995), as evidenced by the

predominance of periods where REW values are lower than the threshold for Mediterranean species (Fig. 2), reported by Granier (1987) and Bréda et al. (1995). Under these conditions, species tend to adjust their water consumption to avoid reaching water potential values that produce a loss of hydraulic conductivity, thus preventing irreversible damage (Vilagrosa et al. 2003a). In this same sense, our results indicate that the species studied show a decrease in Q_{md} according to the decrease in Ψ_{pd} (Fig. 6). Similar results were reported by Goulden (1996) in *Q. agrifolia*, Nadezhdina (1999) in *Malus domestica* Borkh, Stöhr and Lösch (2004) in *F. excelsior*; and more recently in Mediterranean environment by David et al. (2007) in *Q. ilex* and *Q. suber* and Poyatos et al. (2008) in *P. sylvestris* and *Q. pubescent*.

Under soil water deficit conditions (low Ψ_{pd} values), plants can prevent or avoid the impacts of stress in their tissues by using stomatal closure to regulate water loss (Fotelli et al. 2000; Baquedano and Castillo 2006), which, in turn, affects the daily sap flow rate (David et al. 2007; Gartner et al. 2009). In these conditions, the sap flow rate will depend on the plant's water use strategy for coping with water deficit through the drought avoidance mechanisms (water-saving or water-spending), which evidenced in osmotic potential, elasticity of cell walls, capacity of xylem conduits and stomatal control over water loss by transpiration (Levitt 1980; Monson and Smith 1982; Kalapos 1994). A plant follows the water-spenders mechanisms when it shows high stomatal conductance associated with high water losses while maintaining high carbon gain and thus growth (Heilmeier et al. 2002). In contrast, a plant with water-savers mechanisms will display an opposite behaviour, showing strong stomatal regulation to reduce water loss. Both the water-saver and the water-spender mechanisms have been described by Levitt (1980) and have been used by several authors (Dong and Zhang 2001; Vilagrosa 2002; Llorens et al. 2003b; Sakcali and Ozturk 2004).

In this context, under conditions unaffected by water deficit ($\Psi_{pd} > -1.0$ MPa), *P. halepensis* showed high Q_{md} values. However, under water deficit conditions ($\Psi_{pd} < -2.0$ MPa) this species reduced its sap flow rate and registered the lowest Q_{md} of all the species studied (see Fig. 6); we thus classified it as a water-saver species, in agreement with Baquedano and Castillo (2006). Several authors have described *P. halepensis* as very sensitive to water deficit, showing a strong stomatal control under drought conditions (Martínez-Ferri et al. 2000; Baquedano and Castillo 2007), as consequence, we observed that sap flow rate decreased more rapidly in *P. halepensis* than in the shrubs studied (*Q. coccifera* and *P. lentiscus*) when Ψ_{pd} decreased (see Fig. 6). This result tends to confirm the fact that, while conifers regulate their transpiration from $\Psi_{pd} = -1.8$ MPa,

at $\Psi_{pd} = -4.0$ MPa shrubs are still able to carry out osmotic adjustments that allow them to maintain a continuous transpiration in conditions of low soil water availability (Royce and Barbour 2001). This adaptation mechanism of *P. halepensis* by means of water use extremely conservative (water-saver), contribute to this species shows a high drought resistant. Thus jointly with extensive reforestation programs and its reproductive strategy after fire, allows a wide distribution of *P. halepensis* in the Mediterranean basin.

Quercus coccifera showed the highest daily sap flow rate under conditions affected or unaffected by soil water availability (Fig. 6). Unlike *P. halepensis*, this species is able to maintain a high daily sap flow rate regardless of the decline in predawn leaf water potential; showing a water-spending behaviour, which is manifested by a higher stomatal conductance under water deficit conditions (Ksontini et al. 1998; Baquedano and Castillo 2006). Other *Quercus* species (*Q. pubescens*) also tend to show a higher sap flow rate than conifer species (*P. sylvestris*) under drought conditions (Poyatos et al. 2008). *Q. coccifera* is well adapted to semiarid ecosystems, presenting a highly developed root system with shallow roots that enable it to use the water in the top soil as well as deep roots that allow it to extract water reserves from deeper layers (Rambal 1984; Baquedano and Castillo 2007). Nevertheless, some authors have assigned a water saver strategy to this species (Vilagrosa 2002; Sakcali and Ozturk 2004); this may be because these authors used seedlings or young individuals in the measurements.

Erica multiflora presents a shallow root system which favours harnessing the rainwater stored in the top soil (Filella and Peñuelas 2003); however, in a drought period this can be a disadvantage because it cannot explore and use the water sources in the deepest and wettest soil layers. In this sense, this species can show a marked reduction in the gas exchange rate in summer in the absence of changes in shoot water potential; it has thus been considered a drought avoidance species which uses water-savers mechanisms (Llorens et al. 2003b). This evaluation is in agreement with our results.

Pistacia lentiscus has been classified as a drought avoidance species, which under optimum soil water availability and by means of water-spenders mechanisms is capable of maintaining a high stomatal conductance value; however, when water deficit conditions increase, it reduces stomatal conductance and shows a drought avoidance strategy by means of water-savers mechanisms (Vilagrosa 2002). A similar behaviour has been observed in our case. This response of *P. lentiscus* could be due to its shallow root system, as indicated by Filella and Peñuelas (2003).

Stipa tenacissima shows high drought resistance even at very low leaf water potentials (Sánchez 1995; Haase et al.

1999; Domingo et al. 2003). It also shows an opportunistic response to pulse water (Pugnaire et al. 1996) and net water gain, probably because of water vapour adsorption (Ramírez et al. 2007). This theoretical background could explain the relatively high sap flow rates observed in this species in our study. Although we were not able to take joint measurements of sap flow and predawn leaf water potential in this species because of technical difficulties, its high daily sap flow rate, which was almost similar to the one found for *Q. coccifera* on the south-facing slope (Figs. 4, 5), has led us to classify *S. tenacissima* as a water-spender species.

In summary, we found a notable effect of meteorological variables (R_g, T^a, VPD) and water deficit conditions on the sap flow rate. Several meteorological variables showed differences between slope aspect and year of monitoring. Consequently, the species on the south-facing slope showed higher sap flow rates than the species on the north-facing slope. Moreover, the most species also had higher sap flow rates during the wetter year (1998). However, a common seasonal pattern in the sap flow rate by species has been not found, and therefore do not meet one of the initially indicated hypothesis. On the other hand, we were able to link the drought avoidance mechanisms of the different species through the combined use of daily sap flow rate and predawn leaf water potential under different water deficit conditions. Based in this theoretical background, *Pinus halepensis*, *Pistacia lentiscus* and *Erica multiflora* were evaluated as water-saver species, while *Quercus coccifera* and *Stipa tenacissima* were evaluated as water-spender species.

References

Anfodillo T, Rento S, Carraro V, Furlanetto L, Urbinati C, Carrer M (1998) Tree water relations and climatic variations at the alpine timberline: seasonal changes of sap flux and xylem water potential in *Larix decidua* Miller. *Picea abies* (L.) Karst, and *Pinus cembra* L. Ann Sci For 55:159–172

Atzmon N, Moshe Y, Schiller G (2004) Ecophysiological response to severe drought in *Pinus halepensis* Mill. trees of two provenances. Plant Ecol 171:15–22

Badalotti A, Anfodillo T, Grace J (2000) Evidence of osmoregulation in *Larix decidua* at Alpine treeline and comparative responses to water availability of two co-occurring evergreen species. Ann For Sci 57:623–633

Baquedano FJ, Castillo FJ (2006) Comparative ecophysiological effects of drought on seedlings of the Mediterranean water-saver *Pinus halepensis* and water-spenders *Quercus coccifera* and *Quercus ilex*. Trees 20:689–700

Baquedano FJ, Castillo FJ (2007) Drought tolerance in the Mediterranean species *Quercus coccifera*, *Quercus ilex*, *Pinus halepensis* and *Juniperus phoenicea*. Photosynthetica 45(2):229–238

Bautista S, Mayor A, Bourakhouadar J, Bellot J (2007) Plant spatial pattern predicts hillslope runoff and erosion in a semiarid Mediterranean landscape. Ecosystems 10(6):987–998

Bellot J, Ortiz de Urbina JM (2008) Soil water content at the catchment level and plant water status relationships in a Mediterranean *Quercus ilex* forest. J Hydrol 357:67–75

Bellot J, Bonet A, Sánchez JR, Chirino E (2001) Likely effects of land use changes on the runoff and aquifer recharge in a semi-arid landscape using a hydrological model. Landsc Urban Plan 778:1–13

Bonet A, Peña J, Bellot J, Cremades M, Sánchez JR (2001) Changing vegetation structure and landscape patterns in semi-arid Spain. In: Villacampa Y, Brebbia CA, Usó JL (eds) Ecosystems and sustainable development III. WIT Press, Southampton, pp 377–386

Bréda N, Granier A, Aussenac G (1995) Effects of thinning on soil and tree water relations. transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiol 15:295–306

Čermák J, Jeník J, Kučera J, Židek V (1984) Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes of environment. Oecologia 64:145–151

Chirino E (2003) Influencia de las precipitaciones y de la vegetación en el balance hídrico superficial y la recarga de acuíferos en clima semiárido. PhD dissertation, Universidad de Alicante, Spain. (http://rua.ua.es/dspace/handle/10045/3386)

Chirino E, Bonet A, Bellot J, Sánchez JR (2006) Effects of 30-years-old Aleppo pine plantations on runoff, soil erosion, and plant diversity in a semi-arid landscape in south-eastern Spain. Catena 65:19–29

Chirino E, Vilagrosa A, Cortina J, Valdecantos A, Fuentes D, Trubat R, Luis VC, Puértolas J, Bautista S, Baeza J, Peñuelas JL, Vallejo V (2009) Ecological restoration in degraded drylands: the need to improve the seedling quality and site conditions in the field. In: Grossberg SP (ed) Forest management. Nova Science Publisher, New York, pp 85–158

Cohen Y, Cohen S, Cantuarias-Aviles T, Schiller G (2008) Variations in the radial gradient of sap velocity in trunks of forest and fruit trees. Plant Soil 305:49–59. doi:10.1007/s11104-007-9351-0

Conejero W, Alarcón JJ, García-Orellana Y, Abrisqueta JM, Torrecillas A (2007) Daily sap flow and maximum daily trunk shrinkage measurements for diagnosing water stress in early maturing peach trees during the post-harvest period. Tree Physiol 27:81–88

David TS, Henriques MO, Kurz-Besson C, Numes J, Valente F, Vaz M, Pereira JS, Siegwolf R, Chaves MM, Gazarini LC, David JS (2007) Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. Tree Physiol 27:793–803

Di Castri F (1973) Climatographical comparisons between Chile and the western coast of North America. In: Di Castri F, Mooney HA (eds) Mediterranean-type ecosystems: origin and structure. Springer, Berlin

Domingo F, Brenner AJ, Gutiérrez L, Clark, Incoll LD, Aguilera C (2003) Water relations only partly explain the distributions of three perennial plant species in a semi-arid environment. Biol Plant 46(2):257–262

Dong X, Zhang X (2001) Some observations of the adaptations of sandy shrubs to the arid environment in the Mu Us Sandland: leaf water relations and anatomic features. J Arid Environ 48:41–48. doi:10.1006/jare.2000.0700

Dzikiti S, Verreynne J, Stuckens J, Strever A, Verstraeten W, Swennen R, Coppin P (2010) Determining the water status of Satsuma mandarin trees [Citrus Unshiu Marcovitch] using spectral indices and by combining hyperspectral and physiological data. Agric For Meteorol 150(3):369–379

Farrington P, Bartle GA, Watson GD, Salama RB (1994) Long-term transpiration in two eucalypt species in a native woodland estimated by the heat-pulse technique. Austral Ecol 19(1):17–25

Filella I, Peñuelas J (2003) Partitioning of water and nitrogen in co-occurring Mediterranean woody shrub species of different evolutionary history. Oecologia 137:51–61. doi:10.1007/s00442-003-1333-1

Fisher J, Baldocchi D, Misson L, Dawson T, Goldstein A (2007) What the towers don't see at night: nocturnal sap flow in trees and shrubs at two AmeriFlux sites in California. Tree Physiol 27:597–610

Fotelli MN, Radoglou KM, Constantinidou HIA (2000) Water stress response of seedlings of four Mediterranean oak species. Tree Physiol 20:1065–1075

Gartner K, Nadezhdina N, Englisch M, Čermak J, Leitgeb E (2009) Sap flow of birch and Norway spruce during the European heat and drought in summer 2003. For Ecol Manage 258:590–599

Gazal R, Scott R, Goodrich D, Williams D (2006) Controls on transpiration in a semiarid riparian cottonwood forest. Agric For Meteorol 137:56–67. doi:10.1016/j.agrformet.2006.03.02

Goulden ML (1996) Carbon assimilation and water-use efficiency by neighboring Mediterranean-climate oaks that differ in water access. Tree Physiol 16:417–424

Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol 3:309–320

Haase P, Pugnaire FI, Clark SC, Incoll LD (1999) Environmental control of canopy dynamics and photosynthetic rate in the evergreen tussock grass Stipa tenacissima. Plant Ecol 145:327–339

Heilmeier H, Wartinger A, Erhard M, Zimmermann R, Horn R, Schulze ED (2002) Soil drought increases leaf and whole-plant water use of Prunus dulcis grown in the Negev Desert. Oecologia 130:329–336

Infante JM, Domingo F, Fernández-Alés R, Joffre R, Rambla S (2003) Quercus ilex transpiration as affected by a prolonged drought period. Biol Plant 46(1):49–55

Jiménez E, Vega JA, Pérez-Gorostiaga P, Cuiñas P, Fonturbel T, Fernández C, Madrigal C, Hernando C, Guijarro M (2008) Effects of pre-commercial thinning on transpiration in young post-fire maritime pine stands. Forestry 81(4):543–557. doi:10.1093/forestry/cpn032

Kalapos T (1994) Leaf water potential-leaf water deficit relationship for ten species of a semiarid grassland community. Plant Soil 160:105–112

Kramer PJ, Boyer JS (1995) Water relations of plants and soils. Academic Press, San Diego

Ksontini M, Louguet P, Laffray D, Rejeb MN (1998) Comparison of the water stress on stomatal conductance, photosynthesis and growth of Mediterranean oak seedlings (Quercus suber, L., Q. faginea, Q. coccifera) in Tunisia. Ann For Sci 55(4):477–495

Lambs L, Loubiat M, Girel J, Tissier J, Peltier JP, Marigo G (2006) Survival and acclimation of Populus nigra to drier conditions after damming of an alpine river, southeast France. Ann For Sci 63:377–385. doi:10.1051/forest:20006018

Larcher W (1977) Ecofisiología vegetal. Omega, Barcelona

Larcher W (1995) Physiological plant ecology. Springer, Berlin

Levitt J (1980) Responses of plants to environmental stresses, vol 2. Academic Press, New York

Limousin J, Rambal S, Ourcival J, Rocheteau A, Joffre R, Rodriguez-Cortina R (2009) Long-term transpiration change with rainfall decline in a Mediterranean Quercus ilex forest. Glob Change Biol 15(9):2163–2175

Llorens L, Peñuelas J, Estiarte M (2003a) Ecophysiological responses of two Mediterranean shrubs, Erica multiflora and Globularia alypum, to experimentally drier and warmer conditions. Physiol Plant 119:231–243

Llorens L, Peñuelas J, Filella I (2003b) Diurnal and seasonal variations in the photosynthetic performance and water relations of two co-occurring Mediterranean shrubs, Erica multiflora and Globularia alypum. Physiol Plant 118:84–95

Lott J, Khan A, Black R, Ong C (2003) Water use in a Grevillea robusta-maize overstorey agroforestry system in semi-arid Kenya. For Ecol Manage 180:45–59. doi:10.1016/S0378-1127(2)00603-5

Luis VC, Jimenez MS, Morales D, Kucera J, Weises G (2005) Canopy transpiration of a Canary Island pine forest. Agric For Meteorol 135:117–123. doi:10.1016/j.agrformet.2005.11.009

Maestre FT, Huesca M, Zaady E, Bautista S, Cortina J (2002) Infiltration, penetration resistance, and microphytic crust composition in contrasted microsites within a Mediterranean semi-arid steppe. Soil Biol Biochem 34(6):895–898

MaJ Moro, Domingo F, López G (2004) Seasonal transpiration pattern of Phragmites australis in a wetland of semiarid Spain. Hydrol Process 18:213–227. doi:10.1002/hyp.1371

Martínez-Ferri E, Balaguer L, Valladares F, Chico JM, Manrique E (2000) Energy dissipation in drought-avoiding and drought-tolerant tree species at midday during the Mediterranean summer. Tree Physiol 20:131–138

Martínez-Vilalta J, Mangiron M, Ogaya R, Sauret M, Peñuelas J, Piñol J (2003) Sap flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. Tree Physiol 23:747–758

Mediavilla S, Escudero A (2004) Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. Forest Ecol Manage 187:281–294

Mitchell PJ, Veneklaas E, Lambers H, Burgess S (2009) Partitioning of evapotranspiration in a semi-arid eucalypt woodland in south-western Australia. Agric. Forest Meteorol 149:25–37

Monson RK, Smith SD (1982) Season water potential components of Sonoran desert plants. Ecology 63:113–123

Nadezhdina N (1999) Sap flow index as an indicator of plant water status. Tree Physiol 19:885–891

Pfautsch S, Bleby T, Rennenberg H, Adams M (2010) Sap flow measurements reveal influence of temperature and stand structure on water use of Eucalyptus regnans forests. For Ecol Manage 259(6):1190–1199. doi:10.1016/j.foreco.2010.01.006

Poyatos R, Martínez-Vilalta J, Čermák J, Ceulemans R, Granier A, Irvine J, Köstner B, Lagergren F, Meiresonne L, Nadezhdina N, Zimmermann R, Llorens P, Mencuccini M (2007) Plasticity in hydraulic architecture of Scots pine across Eurasia. Oecologia 153:245–259. doi:10.1007/s00442-007-0740-0

Poyatos R, Llorens P, Piñol J, Rubio C (2008) Response of Scots pine (Pinus sylvestris L.) and pubescent oak (Quercus pubescens Willd) to soil and atmospheric water deficits under Mediterranean mountain climate. Ann For Sci 65:306. doi:10.1051/forest:2008003

Pugnaire F, Haase P, Incoll L, Clark SC (1996) Response of the tussock grass Stipa tenacissima to watering in a semi-arid environment. Funct Ecol 10(2):265–274. doi:10.2307/2389852

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

Ramírez D, Valladares F, Blasco A, Bellot J (2006) Assessing transpirations in the tussock grass Stipa tenacissima L.: the crucial role of the interplay between morphology and physiology. Acta Oecol 30(3):386–398. doi:10.1016/jactao.2006.06.006

Ramírez D, Bellot J, Domingo F, Blasco A (2007) Can water responses in *Stipa tenacissima L.* during the summer season be promoted by non-rainfall water gains in soil? Plant Soil 291:67–79. doi:10.10007/s11104-006-9175-3

Royce EB, Barbour MG (2001) Mediterranean climate effects I. Conifer water use across a Sierra Nevada Ecotone. Am J Bot 88(5):911–918

Sakcali MS, Ozturk M (2004) Eco-physiological behaviour of some Mediterranean plants as suitable candidates for reclamation of degraded areas. J Arid Environ 57:1–13. doi:10.1016/S0140-1963(03)00099-5

Salleo S, Nardini A, Lo Gullo MA, Pitt F (2000) Xylem cavitation and control of stomatal conductance in Laurel (*Laurus nobilis* L.). Plant Cell Environ 23(1):71–79

Sánchez G (1995) Arquitectura y dinámica de las matas de esparto (Stipa tenacissima L.); efectos en el medio e interacciones con la erosión. PhD dissertation. Universidad Autónoma de Madrid. Spain

Senock RS, Ham JM (1995) Measurement of water use by prairie grasses with heat balance sap flow gauges. J Range Manage 48:150–158

Steinberg S, McFarland M, Worthington JW (1990) Comparison of trunk and branch sap flow with canopy transpiration in Pecan. J Exp Bot 41(227):653–659

Stocker O (1956) Die Abhängigkeit der transpiration von den Umweltfaktoren. In: Ruthland W (ed) Handbuch der Pflanzenphysiologie III. Springer, Berlin

Stöhr A, Lösch R (2004) Xylem sap flow and drought stress of *Fraxinus excelsior* saplings. Tree Physiol 24:169–180

Terrada J (2001) Ecología de la Vegetación. De la ecofisiología de las plantas a la dinámica de comunidades y paisajes. Omega, Barcelona

Vallejo VR, Alloza JA (2004) La selección de especie en restauración forestal. In: Vallejo VR, Alloza JA (eds) Avances en el estudio de la gestión del monte mediterráneo. Fundación CEAM, Valencia, pp 195–214

van Bavel MG (1984) Flow32^tm Installation and Operation Manual. Version 2.1 software Dynamax Inc., Texas

Vilagrosa A (2002) Estrategias de resistencia al déficit hídrico en *Pistacia lentiscus* L. y *Quercus coccifera* L. Implicaciones en la repoblación forestal. PhD dissertation, Universidad de Alicante, Alicante

Vilagrosa A, Bellot J, Vallejo VR, Gil-Pelegrín E (2003a) Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. J Exp Bot 54(390):2015–2054

Vilagrosa A, Cortina J, Gil-Pelegrín E, Bellot J (2003b) Suitability of drought-preconditioning techniques in Mediterranean climate. Restor Ecol 11(2):208–216

Wang R, Ma L, Xi R, Xu J (2006) Fluctuation of *Acer truncatum* sap flow in rapid growth season and relevant variables. Chin J Ecol 2(3):231–237

Williams D, Cable W, Hultine K, Hoedjes J, Yepez E, Simonneaux V, Er-Raki S, Boulet G, de Bruin J, Chehbouni A, Hartogensis O, Timouk F (2004) Evapotranspiration components determined by stable isotope, sap flow and eddy covariance techniques. Agric For Meteorol 125:241–258. doi:10.1016/j.agromet.2004.04.008

Yue G, Zhao H, Zhang T, Zhao X, Niu L, Drake S (2008) Evaluation of water use of *Caragana microphylla* with the stem heat-balance method in Horqin Sandy Land, Inner Mongolia, China. Agric For Meteorol 148:1668–1678