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Hydraulic lift: soil processes and transpiration in the Mediterranean leguminous shrub *Retama sphaerocarpa* (L.) Boiss

Iván Prieto · Zaal Kikvidze · Francisco I. Pugnaire

Abstract Hydraulic lift (HL) is the process by which plants can passively transfer water from deep, moist soil layers to shallow, dry soil layers. Although it has attracted recent research interest, a mechanistic understanding and its implications for ecosystem functioning are still lacking. Here we describe HL seasonal patterns in a semi-arid shrub species and its influence on plant water dynamics. We measured soil water availability and plant water status over the course of 1 year. Soil water potential in the rhizosphere of *Retama sphaerocarpa* (L.) Boiss (Fabaceae) individuals and in adjacent land was recorded using soil psychrometers. Sap flow was recorded simultaneously using the stem heat balance method (SHBM). Our results show a seasonal HL trend linked to mean seasonal soil water potential with greatest HL amplitudes at moderately low water potentials (ca −4 MPa). HL amplitude was negatively affected by nocturnal transpiration, and HL patterns were recorded in all seasons and at water potentials ranging from −0.1 MPa to −8.5 MPa which is consistent with *R. sphaerocarpa* deep rooting habit and its steady access to ground water.

Abbreviations

HL	Hydraulic lift
SHBM	Stem heat balance method
Ψs	Soil water potential

I. Prieto (✉) · F. I. Pugnaire
Estación Experimental de Zonas Áridas (EEZA),
Consejo Superior de Investigaciones Científicas,
Sacramento s/n, 04120 La Cañada de San Urbano,
(Almería), Spain
e-mail: iprieto@eeza.csic.es

Z. Kikvidze
The University of Tokyo,
#568 Environmental Bldg., 5-1-5 Kashiwanoha,
Kashiwa, Chiba 277-8653, Japan

Introduction

In semi-arid ecosystems water is the most limiting resource (Noy-Meir 1973) being usually scarce and unavailable for plants at least during the peak drought. In water-limited systems some species have developed adaptations such as deep roots that confer them the ability to use water stored in depth when surface soil is dry. This can be crucial during drought and provide deep-rooted species an advantage over shallow-rooted species (Canadell and Zedler 1995). Many plants, however, have developed a dimorphic root system with both deep and superficial roots. This dimorphic morphology spanning different soil layers, and the water potential gradient existing in the soil

between deep wet and shallow dry layers create the conditions for hydraulic lift (HL; Caldwell et al. 1998). HL is the passive movement of water from deep, moist soil layers to dry, superficial soil layers through plant roots (Richards and Caldwell 1987). The mechanism is driven by the water potential (Ψ_s) gradient existing between soil layers when stomata are closed. Thus, water redistributes passively from deep wet layers via root conduits and flows out of roots into the drier shallow soil layers.

The rewetting of surface soil layers at night through HL during drought can improve plant carbon and water balance as plants can take up water from otherwise dry surface soil the next morning (Caldwell and Richards 1989; Dawson 1998). For example, transpiration in a monospecific stand of *Artemisia tridentata* shrubs was improved by up to 20% when HL was operating (Ryel et al. 2002). Caldwell and Richards (1989) found transpiration rates reduced between 25% and 50% in *A. tridentata* shrubs when HL was prevented by nighttime illumination. Other studies have addressed the importance of HL for transpiration both at the community (Lee et al. 2005) and at the individual level (Blum and Jhonson 1992; Caldwell and Richards 1989; Dawson 1996; Ryel et al. 2002). Thus, understanding HL seasonal variation and its relationship with transpiration and soil processes can improve our knowledge on how plants keep water balance.

Most studies published on this topic were carried out under mesic or subxeric conditions (Brooks et al. 2006; Espeleta et al. 2004; Oliveira et al. 2005) while others addressed seasonal patterns in arid or semi-arid phreatophyte and shrub species (Hultine et al. 2003b; Muñoz et al. 2008; Scott et al. 2008). Techniques used to study HL processes range from isotopic determinations using deuterium (^{2}H), or ^{18}O, or a combination of both (Brooks et al. 2006; Burgess et al. 2000) to root sap flow measurements (Nadezhdina et al. 2008) and/or soil psychrometers inserted in the rhizosphere (Muñoz et al. 2008). Few studies, however, have directly linked soil water potential measurements with stem transpiration processes in Mediterranean species (Kurz et al. 2006).

We tested whether *Retama sphaerocarpa* (L.) Boiss performs HL, and tried to establish a seasonal relationship between HL with soil water potential (Ψ_s) and its influence on transpiration processes. *Retama sphaerocarpa* is a phreatophytic leguminous shrub

with evergreen photosynthetic stems (cladodes) that can grow 3 m to 4 m high, and has a dimorphic root system with long surface lateral roots and deep roots that can grow 30 m deep (Haase et al. 1996). This root system allows *R. sphaerocarpa* to tap deep water sources and maintain high photosynthetic rates and high plant water potentials all year round (Haase et al. 1999). We combined the use of soil psychrometers in the rhizosphere of shrubs with sap flow measurements in shrub stems to follow daily and seasonal changes in HL and their implications for plant water balance. The study was performed in a semi-arid system in SE Spain where water is seasonally limiting. We hypothesised that HL in shallow soil layers under *R. sphaercarpa* shrubs changes seasonally in magnitude and influences transpiration processes. Specifically we hypothesised that i) HL magnitude in *R. sphaerocarpa* shrubs is largest during peak drought; ii) the seasonal variation in soil water potential markedly affects HL; and iii) hydraulically-lifted water redistributed to shallow soil horizons would be negatively affected by nighttime transpiration rates.

Materials and methods

Study site and species

The field site is located in the Rambla Honda experimental site, Almería province, SE Spain (37° 108′N, 21° 22′ W, 630 m elevation), a dry valley in the southern aspect of the Sierra de Filabres range, 40 Km north of Almería city. The climate is semi-arid characterised by wet, short winters followed by considerably long summers with scarce or no precipitation at all (Haase et al. 1999). Mean annual precipitation in the area is 250 mm (Lázaro et al. 2001) and mean temperature is 18.2°C (Pugnaire and Lázaro 2000). The soil is from alluvial origin and of a loamy sand texture. The valley is on a michasquist bedrock over which there are extensive alluvial deposits. A detailed description of soil characteristics is given in Puigdefábregas et al. (1996).

The vegetation in the valley bottom is dominated by *Retama sphaerocarpa* (L.) Boiss, a tree-like shrub with photosynthetic stems (cladodes). *Retama sphaerocarpa* is a leguminous shrub growing in NW Africa and in Mediterranean systems in the Iberian Peninsula. It occupies abandoned fields, often form-

ing nearly monospecific savannah-type ecosystems. Its root system is dimorphic, with both extensive lateral roots and a main taproot. Lateral roots are finely branched and can be 15 m long, whereas the taproot is generally devoid of fine branching and may exceed 30 m in depth (Haase et al. 1996). Although not a typical phreatophyte (Haase et al. 1996), its deep rooting habit in the Rambla Honda field site allows R. sphaerocarpa to have access to groundwater all year round as shown by more or less constant water potentials throughout the year (Haase et al. 1999). Open areas among R. sphaerocarpa individuals are barely vegetated, but many herbaceous species are present below the R. sphaerocarpa canopy (Pugnaire et al. 1996). In Rambla Honda R. sphaerocarpa covers 30% of the valley bottom (Pugnaire et al. 2006).

Experimental design

Three R. sphaerocarpa individuals were selected in a plot delimited by a metal fence 80 cm high and inserted 40 cm into the soil to exclude herbivores, mainly small mammals. Two 1 m² plots (hereafter control plots) were established in adjacent soil between shrubs with minimum root influence from R. sphaerocarpa shrubs. Control plots were trenched one meter deep on the side facing the three target R. sphaerocarpa shrubs to avoid root colonization. During the experiment all herbaceous vegetation was periodically removed from the surface of control plots.

Soil water potential (Ψ_s) under the shrubs and in control plots was measured hourly at 30 cm, 50 cm, and 80 cm depth using individually calibrated (Brown and Bartos 1982) thermocouple psychrometers (Wescor PST-55/SF, Logan, Utah, USA). Sensors were set at 30 cm, 50 cm and 80 cm depths in trenches excavated in February 2006 50 cm away from the main trunk and, in order to place them as close as possible to the main root, inserted using 50 cm horizontal tunnels. Sensors were connected to a CR7 data logger (Campbell Scientific Inc., Logan, UT, USA) programmed to register data hourly with a 30 s cooling time to avoid temperature effects. Sensor cables were buried at least 30 cm deep to increase isolation and minimize temperature gradients that could affect readings.

Soil water potential values were corrected for temperature effects using data obtained from control plots. Daily mean soil water potential in these plots was calculated and each hourly value subtracted from the daily mean. The residuals obtained with the calculation were assumed to be caused by temperature effects and were therefore subtracted from data under the shrubs.

Hydraulic lift (HL) was calculated for each depth as the difference between the maximum and minimum water potential during the dark period. The daytime decrease in soil water potential was calculated as the difference between maximum and minimum water potentials during daylight. Following Yoder and Nowak (1999), HL was only considered to occur when water potential increased at night and decreased during daytime and the overnight amplitude was higher than 0.05 MPa.

Sap flow (Q; gh^{-1} water) was measured in one main branch of each of the three shrubs with the steam heat balance method (SHBM). The gauges (Dynagauge, Dynamax Inc, Houston, USA) were placed on randomly selected branches with a diameter of 6–14 mm. The thermal conductance constant (K_{sh}) was calculated individually for each stem/gauge when sap flow was supposed to be minimum, between 12:00 am and 5:00 am for the first 2 days after installation. We used the standard value of 0.42 W m^{-1} K^{-1} for the thermal conductivity of the stem (K_{st}) recommended for woody stems (Van Bavel 1994). Measurements were taken every 60 s, then a mean value averaged every 15 min and a final mean value calculated every half hour. Data were collected half-hourly through a DNX10 logger (Dynamax Inc., Houston, Texas).

Soil water potential and sap flow were measured seasonally from Spring 2006 to Autumn 2007. Summer 2006 was very dry and no water potential measurements were recorded and soil water potential during Autumn 2006 was not recorded due to equipment failure.

Statistical analysis

Repeated measures-ANOVA was used to analyse differences in HL amplitude among seasons. Mean HL amplitude was calculated for a period of 7 days for each season and "Season" was used as the time factor. Autumn 2007 data at 50 cm depth was not used as no HL was detected. The difference in HL at two different depths (30 cm and 50 cm) was analysed

separately as the sphericity assumption in the model was not met and we were not interested in differences between depths within each season. Relationships between variables were examined with mixed model regression using the general regression model (GRM) module in STATISTICA 8.0 (Statsoft, Tulsa, OK, USA). We used "plant" as the random categorical factor in order to account for the variance component responsible for non-independence.

Results

Diel cycles of soil water potential consistent with HL patterns were detected under *R. sphaerocarpa* shrubs at 30 cm and 50 cm depth (Fig. 1a). The overnight variation in soil water potential ($\Delta\Psi_s$) attributed to HL was detected during all seasons at 30 cm and 50 cm. The exceptions were summer and autumn of 2007 at 50 cm depth when, although daily HL patterns were detected, the increases in overnight soil water potential were smaller than 0.05 MPa. HL was never detected at 80 cm during the course of the experiment. At this depth soil water potential remained constant or slowly decreased as soil drying progressed during rainless periods (Fig. 1a). During summer 2007 soil in the upper 50 cm reached very low water potentials (below −5 MPa) that coincided with a steep decline in soil water potential at 80 cm. This suggests that water extraction shifted from shallow to deep layers as drought progressed although HL patterns were not observed at the 80 cm depth. Diel soil water potential fluctuations measured in control plots were generally opposite to HL patterns, as water potential increased during daytime and decreased during nighttime (Fig. 1c). This phenomenon was observed in all seasons and the fluctuations were attributed to temperature effects and thus considered "offset" from the fluctuations typical of HL (Millikin Ishikawa and Bledsoe 2000). Temperature patterns did not differ between control plots and under the shrubs although temperature was slightly higher in control plots (Fig. 1b, d). Observed temperature patterns closely matched the patterns observed in soil water potential in control plots but were opposite to those observed in the rhizosphere of the shrubs (Fig. 1). We detected HL occurring under *R. sphaerocarpa* at water potentials of −0.1 MPa during the wet season

(Fig. 1) and as low as −8.5 MPa during the driest period, summer of 2007. Only after a 27.6 mm precipitation event in spring 2006 did water potential in the top 50 cm of soil increased above −0.1 MPa, which completely inhibited HL (Fig. 2). The HL pattern resumed 4 days later and a second 28 mm rain event on April 28th stopped diurnal HL fluctuations again.

Diel HL cycles matched stomatal closure and consequent transpiration cessation during dark periods as shown by zero or very low sap flow in *R. sphaerocarpa* branches at nighttime (Fig. 3). During dark periods, when transpiration decreased, soil water potential under the shrubs increased until transpiration was restored next morning and soil water potential decreased again.

The magnitude of the overnight increase in soil water potential due to HL ($\Delta\Psi_s$) at 30 cm and 50 cm followed a similar trend over time. However, differences in HL magnitude between seasons were statistically significant only at 50 cm (Table 1). The largest amplitude in diel water potential fluctuations ($\Delta\Psi_s$) occurred during spring 2007 whereas it was smallest in summer 2007 (Fig. 4). Mean seasonal overnight increases in soil water potential correlated with the mean seasonal soil water potential in the top 50 cm of soil ($R^2=0.69$, $p<0.01$, Fig. 4). Maximum fluctuations in soil water potential occurred during spring 2007 at 30 cm and in spring and winter 2007 at 50 cm, when mean soil water potentials ranged from −3 MPa to −5 MPa. HL was minimal at high and low water potentials, during wet periods and summer drought respectively.

The nocturnal increase in soil water potential attributed to HL in shallow layers tightly correlated with the decrease in daytime soil water potential ($\Delta\Psi_s$) the previous day, due to shrub water uptake or evaporation processes (Fig. 5). The slope of the regression equation suggests that nearly 68% of the soil water potential lost during daytime in the top 50 cm of soil was recovered at night through HL.

Nocturnal sap flow was detected in the shrubs in all seasons during some of the nights measured (e.g. Fig. 3). Maximum nighttime sap flow during these periods was negatively correlated with the nocturnal increase in soil water potential (HL) in shallow layers (Fig. 6). When nighttime sap flow was high, HL amplitudes decreased whereas at low nocturnal sap flow values the variation in HL amplitude was much greater.

Fig. 1 Soil water potential and soil temperature diel cycles depicting HL under one *R. sphaerocarpa* representative individual (**a**, **b**) and in a control plot (**c**, **d**) during Spring 2006. *Shaded bars* represent nighttime. *Solid* and *open circles* represent 30 cm and 50 cm depth respectively; *triangles* represent 80 cm depth
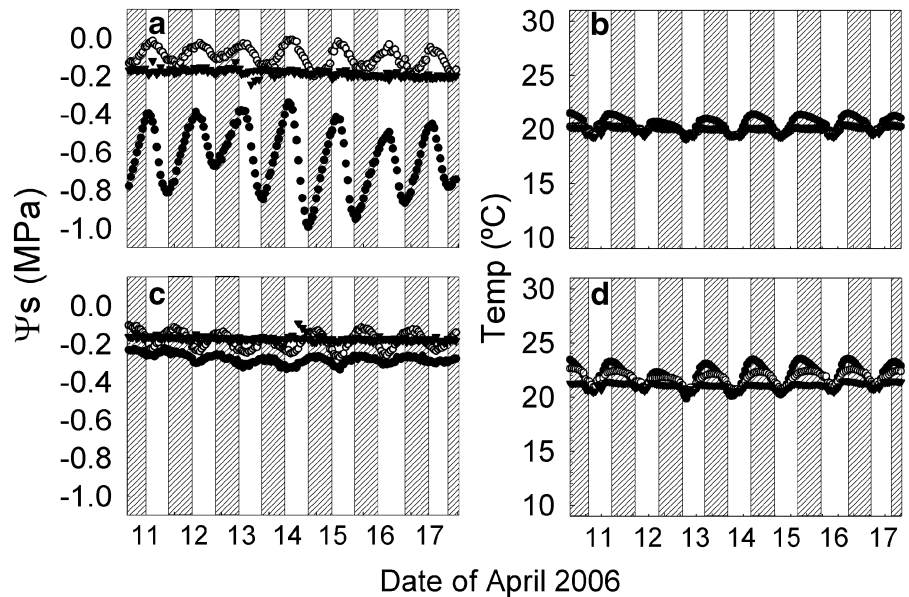
Discussion

HL has been described in several phreatophyte species in arid and semi-arid environments, some of which also performed downward hydraulic redistribution (Burgess et al. 2000; Burgess and Bleby 2006; Hultine et al. 2003a, 2004, 2006; Ludwig et al. 2003; Scott et al. 2008). Our data show that *R. sphaerocarpa* was able to hydraulically lift water from deep to shallow soil layers, as revealed by diel patterns of soil water potential that increased during nighttime

and decreased during daytime. HL in this species was confirmed by parallel measurements in control plots without the influence of *R. sphaerocarpa* shrubs that not only lacked the diurnal pattern but also showed contrasting behaviour due to temperature effects. Sap flow measurements in *R. sphaerocarpa* stems confirmed that HL in this species was related to the decrease of transpiration during dark periods. When the transpiration flow was restored next day, soil water potential decreased again as soil water was being taken up and incorporated to the transpiration stream. Although the maximum nighttime water potential increase ($\Delta\Psi_s$) measured under *R.sphaer-*
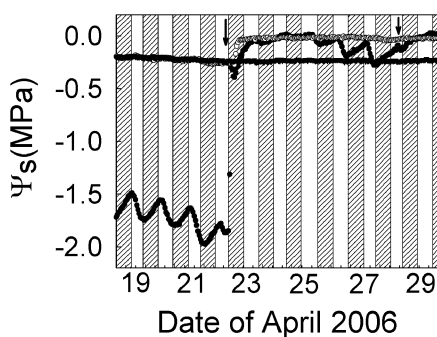

Fig. 2 Soil water potential cycles showing HL under one representative individual of *R.sphaerocarpa* during Spring 2006. Note the rapid cessation of HL cycles for three consecutive days at 30 cm due to the increase in soil water potential after a 27.6 mm and a 28 mm rain event took place on the 22nd and 28th of April (*arrows*). Water did not infiltrate below 50 cm. *Solid* and *open circles* represent 30 cm and 50 cm depth respectively and triangles 80 cm depth
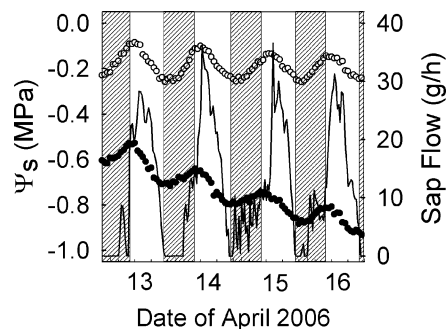

Fig. 3 HL cycles at 30 cm (*solid circles*) and 50 cm (*open circles*) under one representative individual of *R. sphaerocarpa* during spring 2006. Sap flow in one of the main stems is also represented (*solid line*). Nighttime sap flow occurred during some nights as shown by higher than zero values during darkness (*shaded bars*)

Table 1 Repeated measures ANOVA results for HL under *R. sphaerocarpa* shrubs at 30 cm and 50 cm depth during the course of the experiment. Time (Season) used in the analysis were data from spring 2006, and winter, spring, summer and autumn 2007

Depth		df	MS	F	*p* value
30 cm	**Time (Season)**	4	0.01827	0.70123	0.612577
	Error	8	0.026066		
50 cm	**Time (Season)**	3	0.02166	67.155	**<0.001**
	Error	6	0.00032		

Fig. 5 Nighttime increases in soil water potential (*HL*, *MPa*) in three individuals of *R.sphaerocarpa* as a function of daytime changes in soil water potential (*ΔΨ_s*, *MPa*). Night increases in soil water potential (*HL*) were a function of previous day depletion of soil water potential (*ΔΨ_s*). Regression equation is HL (MPa)=0.6825*ΔΨ_s+0.035. Regression is significant at $p < 0.001$

ocarpa shrubs was ca 0.4 MPa (Fig. 4), it is similar to values previously reported in the literature. Nighttime soil water potential increases of 0.4 MPa were recorded under *Artemisia tridentata*, *Helianthus anomalus* and *Quercus laevis* individuals in a greenhouse study (Howard et al. 2009) and soil water potential changes of 0.4 MPa were also reported by Williams et al. (1993) in *Artemisia tridentata* individuals growing in the field. Smaller changes of 0.2 MPa in dry soil (ca −4.5 MPa) were reported for *Adesmia bedwellii* and *Proustia cuneifolia* (Muñoz et al. 2008) and in *Artemisia tridentata* (Richards and Caldwell 1987; Caldwell and Richards 1989).

Since Caldwell and Richards (1989) first suggested that HL could enhance transpiration rates in *A. tridentata*, a number of studies have addressed the influence of HL or hydraulic redistribution on plant water balance of phreatophyte species both experimentally (Burgess et al. 2000) or using models
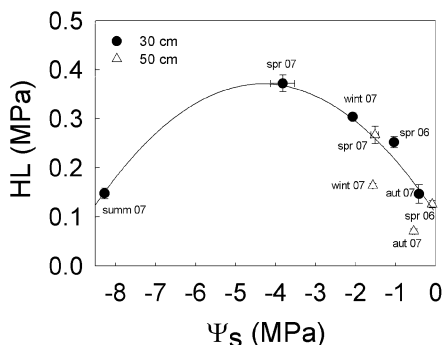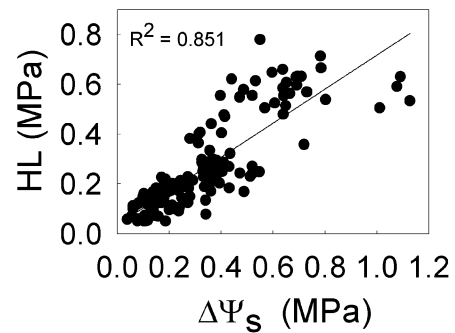
(Amenu and Kumar 2008; Ryel et al. 2002). A correlation between increased transpiration rates and reverse root sap flow was found in *Prosopis velutina* trees suggesting that deep stored water through hydraulic redistribution would allow higher transpiration the next day (Scott et al. 2008). In our field site transpiration by *R. sphaerocarpa* did not correlate with surface soil moisture and suggested an independence of plant water balance from surface soil moisture (Domingo et al. 1999, Haase et al. 1999). In our study, when HL was lowest during summer drought, *R.sphaerocarpa* individuals maintained a positive daytime transpiration rate (data not shown). This suggests our individuals had permanent access to ground water that could maintain transpiration
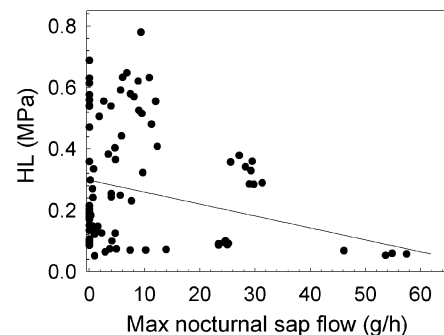

Fig. 4 HL amplitude (*ΔΨ_s*) as a function of soil water potential (*Ψ_s*) in the top 50 cm of soil under *R. sphaerocarpa* shrubs. Seasonal values are Mean±1SE. Regression was significant at $p < 0.01$. (spr = spring; summ = summer; aut = autumn; wint = winter)

Fig. 6 HL (*MPa*) under three individuals of *R. sphaerocarpa* shrubs was negatively influenced by nocturnal transpiration measured as max nocturnal sap flow (g/h) in *R. sphaerocarpa* stems. Solid line indicates the trend of decreasing HL with increasing nighttime sap flow. R^2=0.147, regression was significant at $p < 0.001$

when shallow soil layers were extremely dry and thus create the conditions for HL even during extreme drought.

Hydraulic lift in *R.sphaerocarpa* seemed to be negatively affected by nocturnal sap flow in our shrubs. When sap flow was high during nighttime, HL was reduced but at low nighttime sap flow values HL increased. Hultine et al. (2003b) found a negative relationship between nighttime vapor preassure deficit (D) and reverse sap flow (an indicator of HL) in a lateral root of one tree of the species *Fraxinus velutina*. Another study by Scholz et al. (2008) revealed a negative relationship between nighttime sap flow in the main trunk and reverse sap flow in *Kielmeyera coriacea* when tree leaves were covered. These results, and our own data, are also consistent with a recent study that demonstrated that when nighttime transpiration was suppressed through experimental bagging, HL was enhanced (Howard et al. 2009). To explain the large range of the soil water potential amplitude observed when sap flow was low we hypothesize that, in *R.sphaerocarpa* shrubs, when nocturnal sap flow is low the amount of water that can be released to shallow soil horizons depends more on the water potential gradient between roots and soil or between different soil layers (deep and shallow). However, when nocturnal sap flow is high, the plant and the atmosphere become a sink for hydraulically redistributed water and the water potential gradient existing between deep soil and the plant becomes greater than the gradient between different soil layers which prevents or decreases hydraulic lift in upper soil layers (Hultine et al. 2003b; Scholz et al. 2008). The opposite effect was observed by Wang et al. (2009) that found HL occurring in cotton (*Gossypium hirsutum*) during daytime due to overcast conditions that prevented transpiration and created a gradient between bottom and top layers. With the SHBM used to measure sap flow we were unable to differentiate whether nocturnal sap flow was due to nighttime transpiration or simply to stem tissue water recharge. Nonetheless, in arid environments evaporative demand is high and nighttime transpiration is not uncommon (Dawson et al. 2007). Consistent with Howard et al. (2009) results, our data suggest that nocturnal sap flow, whether caused by nighttime transpiration or rehydration of plant tissues, moderated HL processes by reducing the amount of water redistributed to rhizosphere surface soil. Nighttime has also been hypothe-

sized to increase nutrient uptake, but to date, this last hypothesis remains unconfirmed (Hultine et al. 2003b; Snyder et al. 2008).

Williams et al. (1993) found that the nighttime increase in soil water potential under *A. tridentata* shrubs correlated with soil water depletion the previous day. In our study, HL magnitude under *R. sphaerocarpa* was linearly correlated with soil water depletion the previous day in all seasons. Approximately as much as 68 % of soil water used during daytime was replenished through HL. Overnight soil water recharge through HL is a mechanism that maintains high soil water potentials in upper soil layers (Meinzer et al. 2004). It seems to be driven by water potential gradients (Scholz et al. 2008) and be independent of small variations in daily evapotranspiration, as a rather constant fraction of the water lost from the soil during daytime was replenished at night through HL.

Hydraulic lift has often been hypothesized to occur mostly under drought conditions although Passioura (1988) suggested that HL should likely occur under wet soil conditions. In some published reports, HL amplitudes were higher and occurred more often in dry than in wet periods and increased as drought progressed (Caldwell et al. 1998; Espeleta et al. 2004; Muñoz et al. 2008). This same behaviour was observed when soil water content was measured under *Pseudotsuga meinziesii* and *Tsuga heterophylla* trees, which showed decreasing hydraulic redistribution rates as mean soil water content increased (Meinzer et al. 2007). Higher differences in water potential between soil layers would result in higher redistribution rates, which seem to be generally the case in *R. sphaerocarpa*. In our study, HL amplitude increased until it reached a threshold of −4 MPa, and then decreased again at lower soil water potentials. This supports our second hypothesis that seasonal water potential changes would affect HL. However, contrary to our expectations, when soil water potential reached values as low as −8.5 MPa during summer, HL declined. Most reports of increased HL magnitudes with increasing drought did not measure water potentials below −5 MPa (Ludwig et al. 2003). Under extreme drought conditions, roots dry (Domec et al. 2006) and the water potential gradient between roots and soil decreases, limiting the release of water. Corak et al. (1987) found that increased hydraulic resistance in dry soils could limit water diffusion from

the roots due to factors such as the partial loss of root-soil contact (Nobel and Huang 1992; Vetterlein and Marschner 1993) or partial root death (Caldwell et al. 1998). The fact that we detected HL cycles in summer 2007 suggests that at least some of *R. sphaerocarpa* fine roots in upper soil layers remained active and in contact with soil during extreme drought. The phreatophyte habit of *R. sphaerocarpa* and the access of its deep roots to groundwater (Haase et al. 1999) make the plant able to lift and release water to shallow soil layers during markedly dry periods, helping to maintain fine root activity. This could be an advantage to access nutrients and occasional rain during drought (Bauerle et al. 2008; Richards and Caldwell 1987). Inhibition of HL at high water potentials occurs under some conditions, e.g. after a rain event (Hultine et al. 2004) and we observed that HL cycles ceased after a 26.7 mm rain event occurred on the 22nd of April 2006 when soil water potential rose above −0.1 MPa. The normal diel pattern resumed 4 days later when the soil started to dry, suggesting that soil saturation stops HL. The same response was observed when a second rain event occurred on April 28th. Thus, HL may be an important part of the plant water balance in semi-arid Mediterranean regions where *R. sphaerocarpa* and other shrubs are dominant and play a physiological role in Mediterranean shrub species helping to maintain fine root function in upper soil layers, increasing nutrient uptake during drought or reducing the onset of drought stress (Dawson 1998; Meinzer et al. 2004).

In summary, we found the occurrence of HL in a leguminous shrub from semi-arid SE Spain. We also detected nocturnal sap flow, which may have a negative effect on HL and counter to some extent its positive effect on transpiration. We established the link between HL and next-day soil water depletion as well as the relationship between seasonal HL magnitude and soil water potential. HL could benefit the plant during extreme drought periods by maintaining fine root function in otherwise dry upper soil layers, a mechanism that could also delay the onset of drought stress. However, further research is needed to reveal the interdependence among HL, soil water potential and transpiration processes, and the effect of HL on plant water relations in Mediterranean shrubs.

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