Hydraulic lift through transpiration suppression in shrubs from two arid ecosystems: patterns and control mechanisms

**Iván Prieto · Karina Martínez-Tillería ·
Luis Martínez-Manchego · Sonia Montecinos ·
Francisco I. Pugnaire · Francisco A. Squeo**

Abstract Hydraulic lift (HL) is the passive movement of water through the roots from deep wet to dry shallow soil layers when stomata are closed. HL has been shown in different ecosystems and species, and it depends on plant physiology and soil properties. In this study we explored HL patterns in several arid land shrubs, and developed a simple model to simulate the temporal evolution and magnitude of HL during a soil drying cycle under relatively stable climatic conditions. This model was then used to evaluate the influence of soil texture on the quantity of water lifted by shrubs in different soil types. We conducted transpiration suppression experiments during spring 2005 in Chile and spring 2008 in Spain on five shrub species that performed HL, *Flourensia thurifera, Senna cumingii* and *Pleocarphus revolutus* (Chile), *Retama sphaerocarpa* and *Artemisia barrelieri* (Spain). Shrubs were covered with a black, opaque plastic fabric for a period of 48–72 h, and soil water potential was recorded at different depths under the shrubs. While the shrubs remained covered, water potential continuously increased in shallow soil layers until the cover was removed. The model output indicated that the amount of water lifted by shrubs is heavily dependent on soil texture, as shrubs growing in loamy soils redistributed up to 3.6 times more water than shrubs growing on sandy soils. This could be an important consideration for species growing in soils with different textures, as their ability to perform HL would be context dependent.

Keywords Hydraulic lift · Mediterranean shrubs · Soil texture · Soil water potential · Transpiration suppression

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

K. Martínez-Tillería · F. A. Squeo
Departamento de Biología, Facultad de Ciencias,
Instituto de Ecología y Biodiversidad (IEB),
Universidad de La Serena, Casilla 599, La Serena, Chile

K. Martínez-Tillería · S. Montecinos · F. A. Squeo
Centro de Estudios Avanzados en Zonas Áridas (CEAZA),
La Serena, Chile

L. Martínez-Manchego
Universidad de San Agustín, Arequipa, Peru

S. Montecinos
Universidad de La Serena, La Serena, Chile

Introduction

In arid and semi-arid environments, water is the most limiting resource (Noy-Meir 1973) and plants have developed adaptations such as dimorphic root systems which enable them to switch between shallow and deep water sources depending on availability (Canadell and Zedler 1995; Dawson and Pate 1996; Schenk and Jackson 2002). Deep roots may connect soil layers that differ widely in levels of moisture, and may act as conduits that allow for the passive movement of water following vertical water potential gradients in the soil. This passive movement of water usually takes place between deep, wet soil layers and upper, dry soil layers, and was first described in *Artemisia tridentata* shrubs; it is termed "hydraulic lift (HL)" (Richards and Caldwell 1987). Burgess et al. (1998) used a more comprehensive term for the phenomenon, "hydraulic redistribution (HR)", since

it is now known that water also moves passively through the roots downwards (Burgess et al. 1998, 2001; Ryel et al. 2003) and laterally (Smart et al. 2005).

Hydraulic redistribution has been described in a wide variety of ecosystems, from Mediterranean and semiarid savannahs (Kurz et al. 2006; Nadezhdina et al. 2008) to tropical forests (Meinzer et al. 2004; Oliveira et al. 2005), and involves a wide range of life forms, from woody trees and shrubs (Emerman and Dawson 1996; Squeo et al. 1999; Muñoz et al. 2008) to herbaceous species and crops with shallow roots (Wan et al. 2000; Espeleta et al. 2004). It also happens in a wide range of soil types and textures, from sandy soils (Schulze et al. 1998) to more clayey soils (Ryel et al. 2004). This means that hydraulic redistribution is a widespread phenomenon that seems to be the rule rather than the exception in terrestrial ecosystems. Apart from its importance at the physiological level (Snyder et al. 2008; Warren et al. 2008), the potential effect of this phenomenon has attracted recent attention because of its consequences at the community and ecosystem levels (Lee et al. 2005; Amenu and Kumar 2008; Nadezhdina et al. 2008; Scott et al. 2008). At the ecosystem scale, HL can modify the seasonal microclimate by increasing transpiration during dry periods (Lee et al. 2005). At the community scale, hydraulic redistribution may have positive effects for both the plant lifting water and its neighbours (Hirota et al. 2004; Zou et al. 2005). In a study carried out in upper New York State, a single *Accer sacharum* tree released up to 102 L of water into upper soil layers overnight, which represented 25% of the total amount of water transpired the following day (Dawson 1996). Ryel et al. (2002) demonstrated that *Artemisia tridentata* plants could redistribute up to 19% of the water used for transpiration. Other benefits of lifting water have been described, such as the maintenance of fine root function and mycorrhizal networks under dry conditions (Querejeta et al. 2003; Bauerle et al. 2008) and the prevention of air-induced embolism in roots (Domec et al. 2004), among others. Hydraulic redistribution has also been proposed as a mechanism that buffers soil moisture under shrubs and trees by decreasing the rate at which water is depleted during the drying period. Through a simple simulation, Meinzer et al. (2007) showed that the soil water potential under *Pinus ponderosa* and *Pseudotsuga meinziesii* trees decreased more rapidly when hydraulic redistribution was not operating. This buffering effect could play an important role under conditions of low transpiration demand, such as on cloudy days or during periods of low vapour pressure deficit, and could potentially recharge the upper soil layers through the redistribution of water from deep soil layers.

A number of studies have used transpiration suppression to study the occurrence and effects of hydraulic redistribution on plant water balance and other physiological processes (Caldwell and Richards 1989; William et al.

1993), but few have focused on the effect that suppressed transpiration exerts on water efflux in the soil, its magnitude, and its relationships with soil texture. We explored these issues in an experiment in which, by covering shrubs with wet dark fabric, we attempted to elucidate the pattern of soil recharge by hydraulic redistribution and its magnitude. We developed a new model that accurately simulates HL during short drying cycles (up to 15 days long) under relatively stable climatic conditions. A comparison between field results and theoretical insights gained from our model helped to clarify the relationship between soil texture and hydraulic redistribution. In order to assess differences in hydraulic redistribution patterns among species growing under different conditions but with similar root morphologies and functions, our study was repeated during spring in two different years (2005 and 2008) and at two different sites (Spain and Chile), both of which have a dry Mediterranean-type climate, but which differ in the amount and seasonal pattern of rainfall.

We tested the hypotheses that (1) soil water potential in shallow soils under shrubs with suppressed transpiration increases continuously until transpiration is restored, (2) the amount of hydraulically redistributed water is highly dependent on soil texture, with coarse-textured soils being less conducive to HL than fine-textured soils, and (3) HL patterns differ between sites with different soil textures and annual rainfall regimes.

Methods

Study sites and species

One of the study sites was located in Quebrada El Romeral in the Coquimbo region of north-central Chile (29°43′S–71°14′W, 300 m elevation). The climate of this region is arid Mediterranean, is influenced by coastal fog, and this region has experienced a mean annual precipitation of 76.5 mm over the last 30 years (Squeo et al. 2006). Mean annual temperature is 14.5°C. The soil is of alluvial origin, and has a sandy texture mixed with stones and gravel. The vegetation is a coastal steppe formation with short sclerophyll shrubs covering 20–30% of the soil surface (Olivares and Squeo 1999). The dominant species are *Pleocarphus revolutus* D. Don and *Senna cumingii* (Hook. & Arn.) H.S. Irwin et Barneby in the valley bottoms, whereas the dominant species are *Haplopappus parvifolius* (DC.) A. Gray, *S. cumingii* and *P. revolutus* higher up.

Another study site was located in the lower zone of the Rambla del Saltador, a dry valley on the southern slope of the Sierra de los Filabres range, Almería, SE Spain (37°08′N–2°22′W, 630 m elevation). The climate is semiarid Mediterranean with a mean annual precipitation of

250 mm (Haase et al. 1999). Mean annual temperature is 15.8°C. The soil is of alluvial origin and has a loamy sand texture. The valley is on mica schist bedrock, where erosion has produced large alluvial fans and colluvial deposits (Puigdefábregas et al. 1996). The vegetation is dominated by the shrub *Retama sphaerocarpa* (L.) Boiss., with densities of up to 500 plants per ha (Pugnaire et al. 2006). In gaps among shrubs, vegetation is scant, and most plant biomass is found under the canopy of *R. sphaerocarpa* shrubs (Pugnaire et al. 1996).

The species selected at the Quebrada El Romeral site were two drought-deciduous shrubs, *Flourensia thurifera* (Molina) D.C. and *Senna cumingii* (Hook. & Arn.) H.S. Irwin et Barneby, as well as an evergreen shrub, *Pleocarphus revolutus* D. Don, all of which are endemic to Chile. They all have dimorphic root systems and show evidence of hydraulic lift (León and Squeo 2004). The species selected in Spain were *Retama sphaerocarpa* (L.) Boiss. and *Artemisia barrelieri* Besser. *Retama sphaerocarpa* is an evergreen species with a dimorphic root system that can reach 30 m deep (Haase et al. 1996). *Artemisia barrelieri* is a small evergreen shrub that also has a dimorphic root system, which reaches >1 m deep (I. Prieto, personal observation).

Experimental design

A transpiration suppression experiment was carried out during spring 2005 in Quebrada El Romeral and in spring 2008 in Rambla del Saltador. Four randomly selected individuals of each species were covered with a black, opaque plastic sheet for 48 and 72 h in Chile and Spain, respectively. The cover was installed in a tent-like structure over the shrub. A wet cloth was placed underneath the plastic sheet to avoid overheating the plants. A 15 L container filled with water was placed inside the tents to avoid desiccation.

Soil water potential

Soil water potential (Ψ_s) was recorded using soil psychrometers (PST-55 (-SF); Wescor, Logan, UT, USA) installed 40, 60 and 80 cm deep in Quebrada El Romeral (Chile) and at 30, 50 and 80 cm deep in Rambla del Saltador (Spain). Each sensor was individually calibrated against KCl solutions of known molality (Brown and Bartos 1982). The psychrometers were installed through a soil ditch excavated 50 cm away from the base of the stem. A 50 cm access tube was placed horizontally at each depth, and a psychrometer was inserted through the tube with the intention of leaving it as close as possible to the main root, where we expected that most of the fine roots would be found. The psychrometers were left to stabilize in the soil

for one month. Measurements were taken every hour and automatically recorded in a data logger (CR7, Campbell Scientific Inc., Logan, UT, USA). Data with offset values of greater than ±5 were discarded. The soil water potential was monitored before, during, and after the plants had been covered.

Volumetric water content

The volumetric water content in Quebrada El Romeral was calculated from water potential measurements using the following equation (van Genuchten 1980):

$$\theta_i = \theta_r + \frac{\theta_s - \theta_r}{[1 + |\alpha\Psi_i|^n]^m}, \tag{1}$$

where θ_i = volumetric water content (cm³/cm³) at water potential i; α and n are 0.075 and 1.89, respectively, for sandy soils; $m = 1 - 1/n$; θ_r = residual volumetric water content (cm³/cm³); θ_s = saturated volumetric water content (cm³/cm³); and Ψ_i = soil water potential (MPa).

In Rambla Honda, the volumetric water content was calculated using an experimental equation obtained by plotting different measured soil water content values against measured soil water potential values ($R^2 = 0.9682$, $p < 0.0001$) obtained with the pressure-membrane technique (Richards 1941) using disturbed soil samples:

$$\theta_i = 9.6793 \times e^{(89.4764/(\Psi_i + 59.1755))}, \tag{2}$$

where θ_i = volumetric water content (cm³/cm³) at water potential i and Ψ_i = soil water potential (MPa).

Hydraulic lift model

The soil water potential under shrubs conducting HL showed a sinusoidal trend when plotted as a function of time, which was parameterized with the following equation:

$$\Psi_{s(t)} = \left[\Psi_0 - \frac{\Delta\Psi}{2}\right] + \frac{\Delta\Psi}{2}\cos(2\pi(t - 0.5)) + \alpha(t - 0.5), \tag{3}$$

where $\Psi_{s(t)}$ = soil water potential at time t (days); Ψ_0 = soil water potential at $t = 0.5$ (midday); $\Delta\Psi$ = nocturnal increase in water potential on day t; and α = slope of the straight line obtained from plotting mean daily soil water potentials.

This model allowed us to calculate soil water potentials accurately during a drying cycle with relatively stable climatic conditions for periods as long as 15 days (Martínez-Manchego 2007).

We calculated the increase in soil water potential ($\Delta\Psi_s$) when plants were shaded (referred to as the *observed potential* hereafter, Ψ_{obs}) by subtracting the water potential

measured 24 h after transpiration suppression (Ψ_{obs}) from the soil water potential before the start of transpiration suppression. We used Eq. 3 to calculate the decrease in soil water potential had the plants been left uncovered (termed the *expected potential* hereafter, Ψ_{est}).

Using the equations in Fig. 3, we calculated the difference between the observed and expected water potentials for four different soil water potentials (−1, −2, −4 and −6 MPa). We then calculated the change in volumetric water content for each water potential and soil type; i.e. the amount of water that could potentially be added to the soil during a 24 h period through forced HL. We used the van Genuchten (1980) equation parameters extracted from Hodnett and Tomasella (2002) (Table 1) in order to convert water potential to volumetric water content values for seven different soil types.

Statistical analysis

ANOVA and simple regression analyses were performed using STATISTICA 8.0 (Statsoft Inc. 1984–2008). We performed one-way MANOVA analyses independently for each site (Spain or Chile) with "species" as a factor. As no differences were found among species within each site, a one-way MANOVA with $\Delta\Psi$ (change in soil water potential after 24 h of transpiration suppression) and $\Delta\theta$ (change in volumetric water content after 24 h of transpiration suppression) as independent variables and "species" as the factor, and a one-way MANOVA with $\Delta\Psi$ and $\Delta\theta$ as dependent variables and "site" as the factor were used. $\Delta\theta$ was log-transformed to meet the homogeneity of variance assumption. To evaluate whether the slopes of the two regression lines in Fig. 3 were significantly different, we used the homogeneity of variance assumption option in ANCOVA analysis in STATISTICA 8.0 (Statsoft Inc. 1984–2008). We used Ψ_{est} as the dependent variable and Ψ_{obs} as a covariate.

Results

During the days prior to treatment application, we observed day–night cycles characteristic of HL in all species. Soil water potential in the rhizosphere decreased during the day as water was transpired, and increased at night when transpiration was minimal (Fig. 1). The magnitude of this overnight increase in water potential ($\Delta\Psi_s$) ranged from 0.083 to 0.4 MPa in one individual each of *P. revolutus* and *R. sphaerocarpa*, respectively. These values were always greater than 0.01 MPa and were thus considered to be indicative of HL (Millikin-Ishikawa and Bledsoe 2000). Only in one *A. barrelieri* individual did diel patterns in soil water potential agree with HL patterns; in the other three individuals, such cycles were not detected. This suggests that this species is able to perform HL, and that the lack of response in three of the plants was due to a lack of roots near the sensor (i.e. bad sensor placement). Although HL was detected at all depths measured in *F. thurifera* and *S. cumingii*, at 40 cm in *P. revolutus* and at 30 and 50 cm in *R. sphaerocarpa* and *A. barrelieri* (data not shown), the magnitude of the cycle was greatest at a depth of 30 cm (Spain) or 40 cm (Chile). Hydraulic lift was never detected at 80 cm under *R. sphaerocarpa* or *A. barrelieri* shrubs. Soil water potential profiles measured at different depths under the shrubs prior to treatment application revealed a tendency for increasing water potential with depth. Deep soil layers (below 50–60 cm) had higher water potentials (i.e., were wetter) than shallow soil layers (Fig. 2). Maximum rooting depth and fine rooting depth data (Table 2) show that our shrub species had active fine roots in the upper 60–100 cm of soil, and deep roots (either tap or sinker roots) that can easily reach deeper than 2 m into the soil profile.

When transpiration was artificially suppressed, a continuous increase in rhizosphere water potential was recorded. All five species showed this trend, which continued

Table 1 Soil parameters for the Van Genuchten equation for seven different soil textures

Soil texture	α (kPa^{-1})	SE	n	SE	θ_s (cm^3/cm^3)	SE	θ_r (cm^3/cm^3)	SE
Sand	0.380	0.007	2.474	0.042	0.410	0.002	0.037	0.001
Loamy sand	0.837	0.122	1.672	0.015	0.438	0.003	0.062	0.002
Sandy loam	0.396	0.016	1.553	0.013	0.461	0.005	0.111	0.003
Silt loam	0.246	0.007	1.461	0.013	0.521	0.005	0.155	0.004
Loam	0.191	0.006	1.644	0.027	0.601	0.005	0.223	0.005
Clay loam	0.392	0.015	1.437	0.008	0.519	0.006	0.226	0.003
Clay	0.463	0.022	1.514	0.029	0.546	0.004	0.267	0.004

Standard errors (SE) were calculated from the standard deviation (SD) in Hodnett and Tomasella (2002), and $n = 497$. α and n are shape parameters for the Van Genuchten soil water curve, and θ_s and θ_r are the saturated and residual volumetric water contents (cm^3/cm^3), respectively

Modified from Hodnett and Tomasella (2002)

Fig. 1 Soil water potential (Ψ_s) measured at 30 cm depth under representative individuals of *Retama sphaerocarpa* (**a**) and *Artemisia barrelieri* (**b**) in Spain and at 40 cm depth under representative individuals of *Flourensia thurifera* (**c**) and *Senna cumingii* (**d**) in Chile. *Solid lines* represent the measured water potential and *dashed lines* represent modelled hydraulic lift patterns in the absence of transpiration suppression. *Thin grey bars* represent nighttime periods and *thick grey bars* represent the period when the plants were covered. All of the plants were subjected to transpiration suppression (*thick grey bars*). Note the different scales on the y-axes
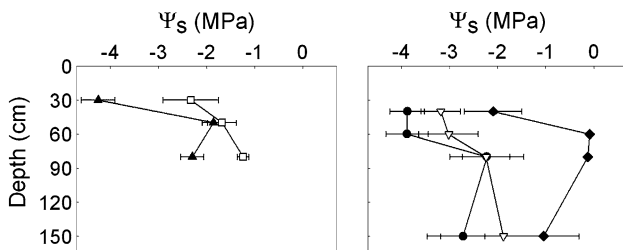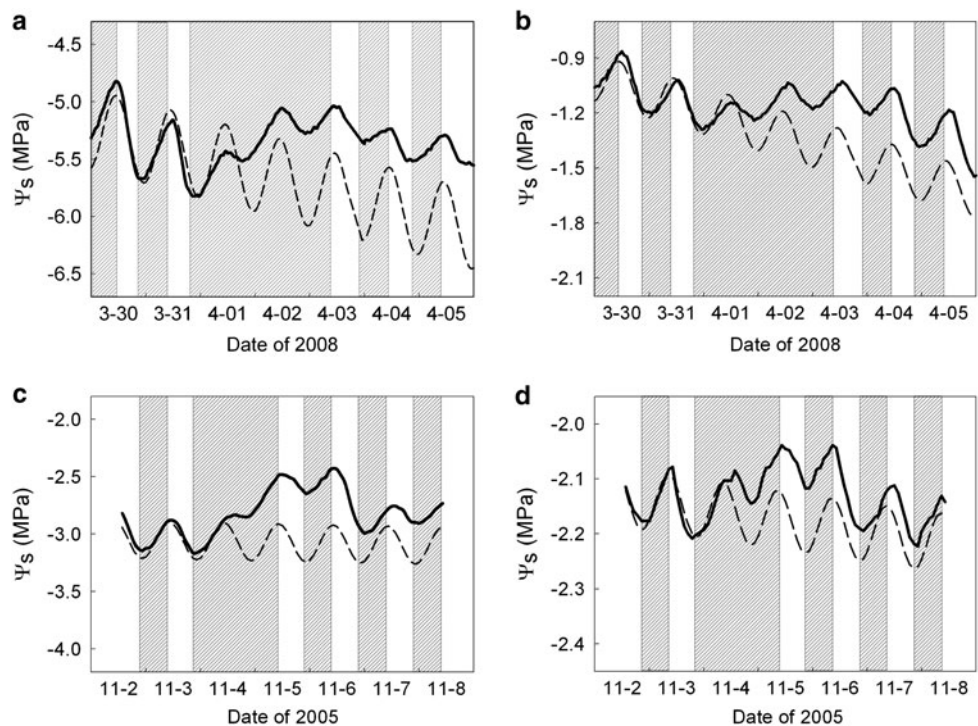

Fig. 2 Soil water potential (Ψ_s) measured within the rhizosphere under individuals of the species under study one day before the transpiration suppression treatment took place ($n = 4$, except for *S. cumingii*, where $n = 3$ at 80 cm and $n = 2$ at 150 cm, and for *P. revolutus*, where $n = 2$ at 40 cm and $n = 1$ at 60, 80 and 150 cm). *Left panel* depicts the Spanish species *Retama sphaerocarpa* (*solid triangles*) and *Artemisia barrelieri* (*open squares*); *right panel* depicts the Chilean species *Flourensia thurifera* (*solid circles*), *Senna cumingii* (*open triangles*) and *Pleocarphus revolutus* (*solid diamonds*)

Table 2 Rooting depth data for the five species included in the study

Species	Site	Max root depth	Max fine root depth	Source
F. thurifera	Chile	>2 m	0.95 m	Olivares (2003)
P. revolutus	Chile	>2 m	0.68 m	Olivares (2003)
S. cumingii	Chile	>2 m	1.08 m	Olivares (2003)
R. sphaerocarpa	Spain	>20 m	>0.60 m	Haase et al. (1996)
A. barrelieri	Spain	>1 m	n.a.	Root excavation

n.a., not available

for 48 h in *F. thurifera*, *S. cumingii* and *P. revolutus*, and for 72 h in *R. sphaerocarpa* and *A. barrelieri*; i.e. the whole period that plants were covered. A small decrease in soil water potential was observed, however, during daylight periods when the plants were covered (Fig. 1). The mean increase in rhizosphere water potential 24 h after transpiration suppression ranged from 0.32 ($\pm$0.092) MPa in *R. sphaerocarpa* to 0.13 ($\pm$0.086) MPa in *P. revolutus*. This rise in soil water potential resulted in an increase in volumetric water content under the shrubs, which was greatest under one individual of *A. barrelieri*, with a total of 1.13×10^{-3} cm³/cm³ of water lifted, and least under *R. sphaerocarpa*, with a mean total of 1.24×10^{-4}

($\pm 2.6 \times 10^{-5}$) cm³/cm³ (Table 3). Neither changes in soil water potential ($\Delta\Psi$) nor changes in volumetric water content ($\Delta\theta$) were significantly different among species (MANOVA, $F_{8,24} = 1.334$, $p = 0.27$) or sites (MANOVA, $F_{2,12} = 1.158$, $p = 0.346$).

A linear relationship was found between the estimated and observed soil water potentials before (solid circles in Fig. 3) and 24 h after transpiration suppression (clear circles in Fig. 3). Before transpiration suppression, the regression line was 1:1, since values estimated using Eq. 3 and measured values were very close ($R^2 = 0.998$, $p < 0.001$). This suggests that the equation developed to reproduce HL patterns (Eq. 3) was accurate when predicting soil water potentials. After being covered for 24 h there was a deviation from the 1:1 line, showing that observed water potentials were higher (less negative) than expected ($R^2 = 0.989$, $p < 0.001$). The slopes of the two regression lines were significantly different (ANCOVA,

Table 3 Soil water potential and volumetric water content at 30 cm and 40 cm in Spain and Chile, respectively, before transpiration suppression (Ψ_{obs}; θ_{obs}) and 24 h after transpiration suppression (Ψ_a; θ_a)

Species	Site	Ψ_a (MPa)	Ψ_{obs} (MPa)	Ψ_{est} (MPa)	$\Psi_{obs} - \Psi_{est}$ (MPa)	θ_a (cm³/cm³)	θ_{obs} (cm³/cm³)	θ_{est} (cm³/cm³)	$\theta_{obs} - \theta_{est}$ (cm³/cm³)
F. thurifera	Chile	−4.11 (±0.33)	−3.90 (±0.38)	−4.13 (±0.33)	0.23 (±0.055)	2.480 × 10⁻³ (±2.00 × 10⁻⁴)	2.590 × 10⁻³ (±2.57 × 10⁻⁴)	2.439 × 10⁻³ (±1.93 × 10⁻⁴)	1.51 × 10⁻⁴ (±1.62 × 10⁻⁵)
P. revolutus	Chile	−2.12 (±0.33)	−2.12 (±0.49)	−2.25 (±0.57)	0.13 (±0.086)	4.643 × 10⁻³ (±1.14 × 10⁻³)	4.547 × 10⁻³ (±9.37 × 10⁻⁴)	4.357 × 10⁻³ (±9.95 × 10⁻⁴)	1.90 × 10⁻⁴ (±5.85 × 10⁻⁵)
S. cumingii	Chile	−3.24 (±0.54)	−3.13 (±0.58)	−3.32 (±0.56)	0.22 (±0.080)	3.193 × 10⁻³ (±4.62 × 10⁻⁴)	3.333 × 10⁻³ (±4.97 × 10⁻⁴)	3.159 × 10⁻³ (±4.82 × 10⁻⁴)	1.74 × 10⁻⁴ (±1.62 × 10⁻⁵)
R. sphaerocarpa	Spain	−4.49 (±0.45)	−4.41 (±0.70)	−4.73 (±0.74)	0.32 (±0.092)	9.876 × 10⁻² (±1.7 × 10⁻⁴)	9.878 × 10⁻² (±1.5 × 10⁻⁴)	9.866 × 10⁻² (±1.6 × 10⁻⁴)	1.24 × 10⁻⁴ (±2.6 × 10⁻⁵)
A. barrelieri	Spain	−1.29	−1.23	−1.47	0.24	10.3427 × 10⁻²	10.3751 × 10⁻²	10.2623 × 10⁻²	1.13 × 10⁻³

Estimated water potential was calculated from our model using Eq. 3 after 24 h of transpiration suppression (Ψ_{est}). Estimated water content 24 h after transpiration suppression (θ_{est}) was calculated from Ψ_{est} values using Eqs. 1 and 2 for Chile and Spain, respectively (see "Methods"). Values for Chilean (*F. thurifera*, *P. revolutus* and *S. cumingii*) and Spanish (*R. sphaerocarpa* and *A. barrelieri*) species are presented. A positive value of the difference between observed and estimated values ($\Psi_{obs} - \Psi_{est}$ and $\theta_{obs} - \theta_{est}$) indicates that water was released into the soil. Data are mean ± 1 SE, $n = 4$, except for *P. revolutus* ($n = 2$) and *A. barrelieri* ($n = 1$)
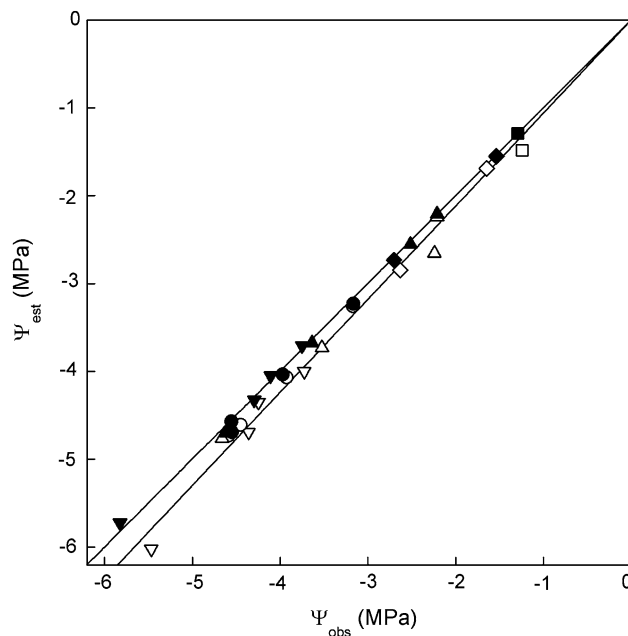
Fig. 3 Estimated versus observed soil water potentials measured in the rhizospheres of five shrub species in Chile and Spain before (*solid symbols*) and after (*open symbols*) suppressed transpiration. *Regression lines* are shown. Regression equations were $\Psi_{est} = 0.9993 \times \Psi_{obs}$ ($R^2 = 0.998$; $p < 0.001$) and $\Psi_{est} = 1.0597 \times \Psi_{obs}$ ($R^2 = 0.989$; $p < 0.001$), respectively. Legend as in Fig. 2

$F_{1,40} = 8.273$, $p < 0.01$), and at any given soil water potential, the difference between both lines represented the increase in water potential due to HL when transpiration was suppressed. Differences became greater as soil water potentials decreased, being greatest in the driest soils (around −6 MPa, Fig. 3).

According to calculations in our model, the amount of water that plants could potentially shed into the rhizosphere through HL ($\Delta\theta_s$) is always greater in loamy soils (Fig. 4), indicating that these soil types may be able to store a larger amount of water through HL. The amount of water lifted in sandy soils was about five times smaller than in loamy soils at all water potentials. For any given soil type, the amount of water stored in shallow soil layers through HL was greater in moderately dry soil (−1 MPa), and decreased sharply as soils dried out (Fig. 5).

Discussion

We have identified five species characteristic of arid Mediterranean-type climates that were able to perform HL. The daily cycles of soil water potential measured in the rhizospheres of these shrubs were indicative of their ability to lift water from deep soil layers and release it into upper, dry soil layers at night, resulting in an increase in soil water potential. We cannot provide isotopic evidence of deep
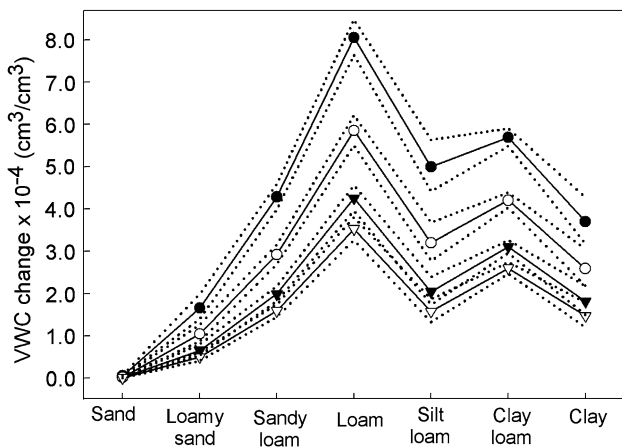
Fig. 4 Soil volumetric water content change (VWC) due to HL for seven soil types differing in texture calculated at four different soil water potentials: −1 MPa (*solid circle*), −2 MPa (*open circles*), −4 MPa (*solid triangles*) and −6 MPa (*open triangles*). Values were calculated from the regression equations in Fig. 3 and using van Genuchten's (1980) soil parameter values for the different textures (see "Methods" and Table 3). *Dotted lines* represent 95% confidence intervals for the curves
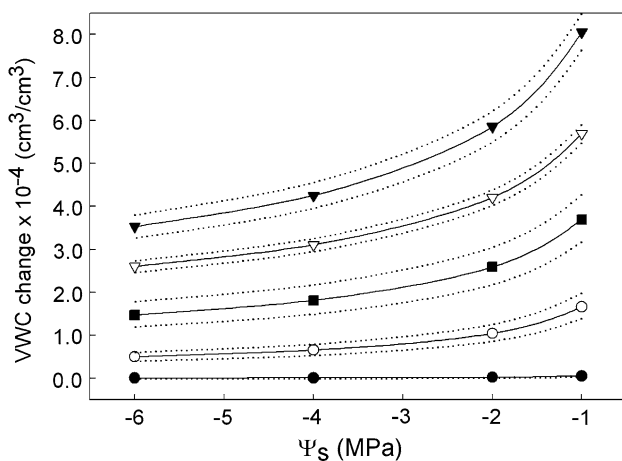

Fig. 5 Soil volumetric water content change due to HL in a range of soil water potentials for five soil types differing in texture: sand (*solid circle*), loamy sand (*open circle*), loam (*solid triangle*), clay loam (*open triangles*) and clay (*solid square*). Values were calculated from the regression equations in Fig. 3 and using van Genuchten's (1980) soil parameter values for the different textures (see "Methods" and Table 3). *Dotted lines* represent 95% confidence intervals for the curves. When they are smaller than the symbols, the 95% intervals are not shown

water being released into shallow soil layers. However, the diel HL cycles observed in shallow soil layers and the continuous increase in soil water potential while the individuals remained covered, along with soil water potentials and root distribution profiles, strongly suggest that plants were tapping deep, wet soil layers, and that these were the sources of water that was hydraulically lifted into shallow layers during dark periods.

In shallow soil layers, a continuous increase in water potential was observed in the rhizospheres of shrubs when transpiration was experimentally suppressed, thus confirming that stomatal closure is the trigger for HL. This supports our hypothesis that water potential continuously increases in the soil through HL until transpiration is restored and the soil–plant–atmosphere continuum is re-established. The small depressions in soil water potential observed when plants were covered could be due to the less than completely opaque nature of the fabric used, or small openings in the tents that were constructed, which may have allowed some light into the structures. However, covering the plants most likely resulted in a decreased vapor pressure deficit through increased relative humidity, which may have enhanced the process of HL (Howard et al. 2009).

The increase in soil water potential during prolonged periods of low transpiration can be of importance in plant communities performing HL. During periods of low evaporative demand (e.g., at night or on cloudy days), water may move from the plant to the soil, helping to recharge water into shallow layers, which could then enhance transpiration rates (Caldwell and Richards 1989; William et al. 1993), buffer or delay the onset of drought stress (Meinzer et al. 2007), or extend mycorrhizal and fine root survival during drought (Querejeta et al. 2003, 2007; Bauerle et al. 2008).

Despite differences in soil texture and annual rainfall between our two field sites, the amount of water released into shallow soil through HL during suppressed transpiration was not statistically different between sites, thus rejecting our hypothesis that differences between sites would modify HL patterns and their magnitudes. We expected differences in HL as soil texture varied between sites, but the results of our model indicated that there was a similar magnitude of HL in sandy and loamy sand soils (Fig. 5), which might explain why differences in HL between sites were minimal. However, the low number of replicates used in the analysis might have reduced the sensitivity of the tests, as differences in overnight increase in soil water potential were apparent between species at the two sites [0.32 (±0.092) MPa in *R. sphaerocarpa* vs. 0.13 (±0.086) MPa in *P. revolutus*].

We developed a model that accurately simulates HL for periods of up to 15 days during a drying cycle. The model allowed soil water potential changes to be compared between plant species under suppressed transpiration conditions. Other numerical models of HL have been used for general predictions or longer periods (Mendel et al. 2002; Siqueira et al. 2008). However, our model is very useful for short-term accurate predictions of soil water potential, and can be used as a tool in manipulative HL studies that usually lack control treatments.

Through our model we were able to predict the variation in HL (measured as a difference in volumetric water content, $\Delta\theta_s$) in a range of soil textures from coarse (sand) to heavy textured (clay) soils at four different water potentials. A smaller variation in soil water content due to HL occurred in sandy soils than in loamy soils at any soil water potential. Loamy soils have a texture finer than sand, and thus the amount of water that they can hold is greater. Sandy soils usually have steeper soil moisture release curves, as indicated by greater *n* values in their Van Genuchten (1980) soil curves (Hodnett and Tomasella 2002). This suggests that water is lost rapidly while there is only a small decrease in water potential. In addition, loamy soils can also store water in a form that is more readily available to plants than finer-textured soils (Bristow 1984), which may allow for greater water movement between roots and soil. Water in clayish soils is tightly bound to soil particles, so greater water potentials are needed for the plant to take up the water (Sperry and Hacke 2002). On the other hand, coarse-textured soils (sandy, loamy sand or sandy loam) usually have lower field capacities (lower θ_s values) and thus are less able to hold large amounts of water (Hillel 2004; Bristow 1984). Consistent with other reports, the amount of water that can potentially be redistributed into the soil is thus dependent on soil texture, with coarse-textured soils being less conducive to HL (Yoder and Nowak, 1999; Hultine et al. 2006; Siqueira et al. 2008; Wang et al. 2009). The relationship with texture becomes nonlinear in more clayish soil types, which have intermediate properties between sandy and loamy soils regarding HL. Yoder and Nowak (1999) found a negative relationship between HL and the percentage of sand particles present in the soil, but they only measured HL in species growing in soils with more than 60% sand (sandy soils), and thus the linear relationship they found might be caused by the narrow range of soils used in their study. They attributed this effect to a loss of root–soil contact, although factors such as decreased hydraulic conductivity and increased fine root mortality at low soil water potentials likely played a role too. Although we did not measure root conductivity or other physiological or morphological variables, our approach can shed light on the physical influence of soil texture on the total amount of water that plants can transport from deep, wet soils to shallow, dry soil layers, which strongly depends on the type of soil they are growing in (Fig. 5).

Soil texture can also influence plant traits such as root morphology (Sperry and Hacke 2002), root and shoot hydraulic conductance (Hultine et al. 2006) and other functional aspects (e.g. abundance of active fine roots and mycorrhizae) that have been shown to influence hydraulic redistribution patterns (Querejeta et al. 2003; Domec et al. 2004; Scholz et al. 2008). Although we did not include

these factors in our modelling approach, our results are consistent with previously reported differences in HL patterns and magnitudes between soils of different textures (Yoder and Nowak 1999; Aanderud and Richards 2009). Wang et al. (2009) reported greater HL in the rhizospheres of cotton plants growing in clayey soils than in plants growing in sandy soils. They also reported that HL lasted longer in clayey soils. In yet another study, Aanderud and Richards (2009) measured greater increases in overnight soil water potential in *Artemisia tridentata* shrubs growing in loamy sand soils (75% sand fraction) than in *Sarcobatus vermiculatus* individuals growing in sandy soils (92% sand fraction). Although we are aware that our model may be an oversimplification of the HL phenomenon, and, as stated above, that other factors might influence HL patterns or magnitudes, the consistency between our modelled results and previous reports leads us to believe that our approach is useful for understanding the influence of soil texture on HL.

Soil water potential gradients are the main factor driving water redistribution by plants (Meinzer 2004; Scholz 2008), regardless of soil texture or root traits (Siqueira et al. 2008). We found that the quantity of water released though HL into shallow soil layers was minimal when these layers were very dry (−4 to −6 MPa), whereas more water could be redistributed into moderately dry upper soil layers (−1 MPa), even though the soil water potential gradient was smaller. Similar results were also found under *R. sphaerocarpa* shrubs in the same area by Prieto et al. (2010). An explanation could be the nonlinear relationship between soil water potential and soil water content, which in our model resulted in decreased HL magnitude at low water potentials (see Figs. 4, 5). The large gradients in soil water potential present during drought resulted in the release of smaller amounts of water into the top soil layers under *R. sphaerocarpa* (Prieto et al. 2010). Nonetheless, factors such as a decrease in root hydraulic conductivity or a loss of root–soil contact can also explain the sharp decrease in HL rates in very dry soils (Domec et al. 2004; Warren et al. 2007). The process of HL generally ceases at soil water potentials ranging from −1.3 MPa in *Gossypium hirsutum* (Baker and van Bavel 1988) to −5.0 MPa in *Acacia tortilis* (Ludwig et al. 2003). We measured HL, however, at water potentials of ca. −6 MPa in *R. sphaerocarpa*, which suggests that this species has active roots in shallow soil layers at rather low water potentials (Prieto et al. 2010). These results also suggest that the soil water potential at which HL ceases might be species specific. Not only water potential but also a combination of soil parameters (i.e. soil texture or water-holding capacity, among others) along with plant morphological and physiological traits (e.g. root density and mortality, root hydraulic conductivity) may determine the quantity of

water released by HL. This could be an important consideration for species growing in soils with different textures, as their ability to perform HL would be context dependent.

Our results clearly show that shrubs can keep redistributing water from deep, wet layers into shallow soil layers during suppressed transpiration, at least for short periods (48–72 h). In *R. sphaerocarpa*, this phenomenon occurred for more than 72 h after the onset of the artificial dark period. Although we did not measure transpiration rates, previous studies have modelled the importance of HL for sustaining transpiration during dry periods (Siqueira et al. 2008). The extra water released into the soil through HL could enhance transpiration and thus have a beneficial effect on plant water balance and carbon fixation (Caldwell et al. 1998; Lee et al. 2005), although this effect is unlikely in our species, as the amount of water redistributed to the upper soil layers was generally low. HL accounted for only 3% of the total transpired water in *Artemisia tridentata* during summer drought (Ryel et al. 2002). Due to the low soil water potentials measured during our measurement period, the effect of HL on our shrub species probably plays a role in the maintenance of fine root structure and function during drought (Bauerle et al. 2008; Caldwell et al. 1998), extending the survival of associated mycorrhizae (Querejeta et al. 2007; 2009), or lowering root xylem cavitation (Domec et al. 2004). This phenomenon can be of great importance in sandy soils, as shrubs usually experience a higher vulnerability to xylem cavitation (Sperry and Hacke 2002). In leguminous shrub species, HL could also help maintain associated N-fixing bacteria (Athar and Jhonson 1997; Swaine et al. 2007) by mitigating decreased soil water potentials during drought (Meinzer et al. 2004).

In summary, we found a new species that performs HL in arid systems. We also accurately simulated HL patterns using a simple model that can be a useful tool for studying HL effects at the community level; importantly, we found a correlation between soil texture and the volume of water redistributed, and that HL was more efficient when the upper layers were moderately dry than when they were very dry. Soil texture and soil water potential may be more important than species-specific traits in determining the amount of water released into the soil.

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