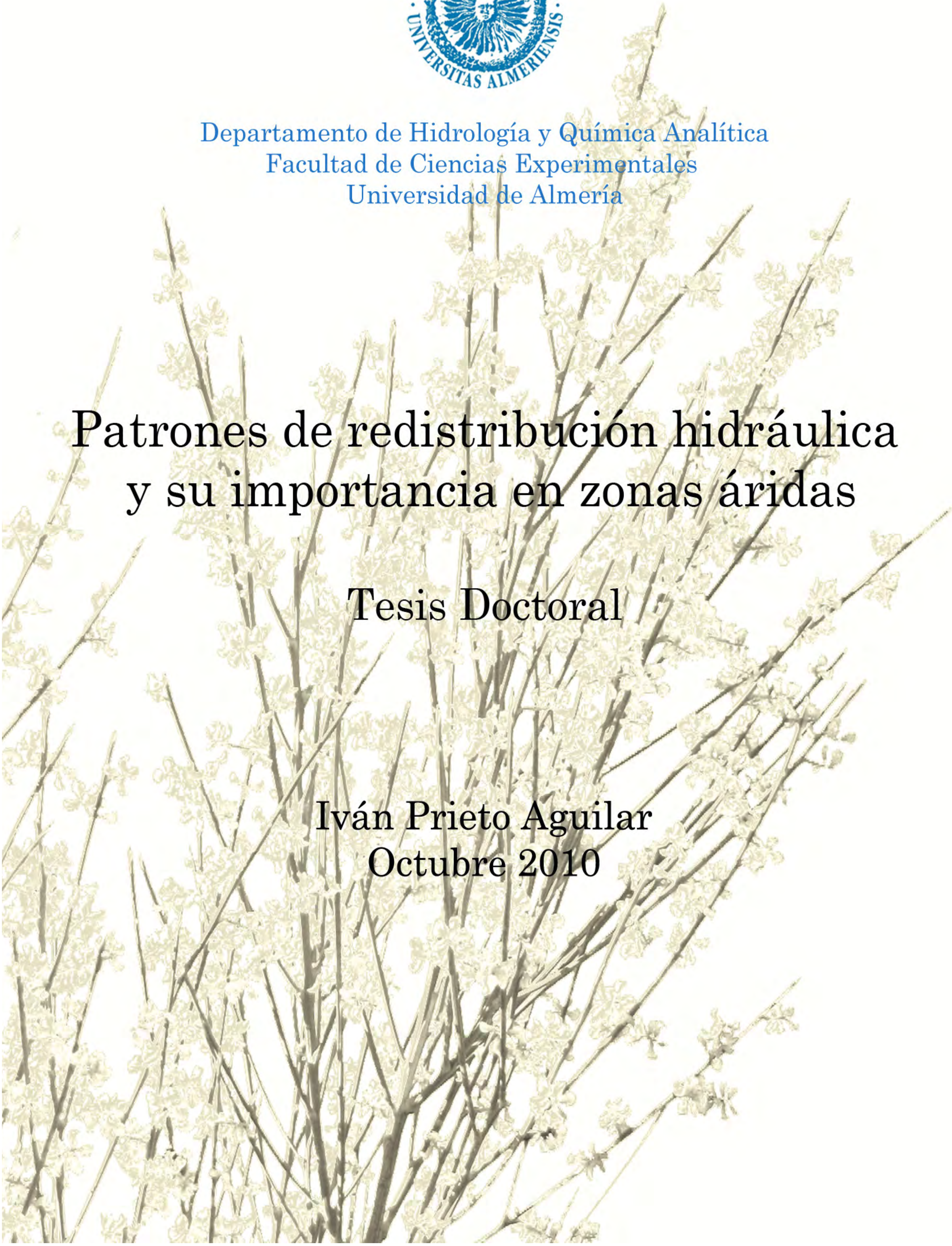

Departamento de Hidrología y Química Analítica
Facultad de Ciencias Experimentales
Universidad de Almería

Patrones de redistribución hidráulica y su importancia en zonas áridas

Tesis Doctoral

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Departamento de Hidrología y Química Analítica
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Memoria de Tesis Doctoral presentada por **Iván Prieto Aguilar** para la obtención del grado de Doctor en Ciencías Biológicas por la Universidad de Almería

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A mi familia y a Noelia

A Roberto†

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Patrones de redistribucion hidráulica y su importancia en zonas áridas

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Introducción

PATRONES DE REDISTRIBUCIÓN HIDRÁULICA Y SU IMPORTANCIA EN ZONAS ÁRIDAS

Introducción General

El agua es el principal factor limitante en ecosistemas áridos y semi-áridos (Noy-Meir 1973). Diversos mecanismos hacen posible que plantas de medios desérticos y semi-desérticos hagan un uso eficiente de cantidades limitadas de agua (véase, por ejemplo, Ehleringer et al. 1999). Por otra parte, hay otros factores como la textura y el nivel de desarrollo del suelo, el micro-clima creado por la vegetación, o la interferencia y facilitación tanto intra- como inter-específica que influyen significativamente en el uso que hacen del agua plantas individuales. No obstante, en zonas áridas se ha visto que la redistribución hidráulica (RH) juega un papel que puede ser decisivo en el balance hídrico no sólo de la planta levantadora (Caldwell and Richards 1989; Ryel et al. 2002) sino de comunidades o ecosistemas enteros (Jackson et al. 2000; Lee et al. 2005), o incluso, a un nivel más específico, para las plantas que crecen cerca de la zona de influencia de plantas levantadoras (Caldwell and Richards 1989; Dawson 1993; Ludwig et al. 2004).

El fenómeno de la redistribución hidráulica fue descrito por primera vez como "levantamiento hidráulico" (Richards et al. 1987). El levantamiento hidráulico es el transporte del agua por medio de las raíces desde capas profundas y húmedas del suelo a capas más superficiales y más secas. Las raíces actúan como meros conductos para el agua, facilitando su difusión de unas capas del suelo húmedas a otras más secas sin suponer un gasto de energía metabólica para la planta levantadora. De esta forma, el ascenso de agua de capas profundas y húmedas a capas más superficiales y secas se genera de forma pasiva por el gradiente de potencial hídrico generado por las diferencias de humedad entre las diferentes capas de suelo. Este fenómeno se produce mientras los estomas de la planta están cerrados (León & Squeo 2004), hecho que en la mayoría de las especies ocurre durante la noche. Sin embargo, en plantas con metabolismo tipo CAM los patrones se invierten produciéndose el levantamiento hidráulico durante el día, cuando la planta tiene los estomas cerrados (Yoder & Nowak 1999). Con los estomas abiertos en la planta, se establece un gradiente de potencial hídrico entre el suelo y la atmósfera que hace que el agua fluya en el contínuo suelo-planta-atmósfera de mayor a menor potencial hídrico (Sperry 2000). Durante la noche (durante el día en especies con metabolismo tipo CAM), con los estomas cerrados, el contínuo suelo-planta-atmósfera se rompe generandose un gradiente de potencial entre las diferentes capas del suelo. Así, el agua se mueve a través de las raíces de zonas de mayor potencial hídrico (capas húmedas) a zonas de menor potential hídrico (capas secas). También se ha detectado levantamiento hidráulico durante el día en algunas especies cuando se produce un cierre diurno de los estomas para compensar el estrés hídrico y lumínico, lo que se conoce como "cierre estomático" (Espeleta et al. 2004) o bajo supresión artificial de la transpiración (Howard et al. 2009; Richards and Caldwell 1987). El fenómeno también ocurre de forma lateral (Smart et al. 2005) e inversa hacia capas más profundas del suelo (Burgess et al. 2000; Burgess et al. 1998; Ryel et al. 2003). A todos estos procesos se les dio el nombre genérico de redistribución hidráulica (RH) (Burgess et al. 1998).

La redistribución hidráulica se ha observado sobre todo en ambientes áridos (Caldwell et al. 1998; Jackson et al. 2000) tales como la zona árida y fría de la Gran Pradera americana (Donovan & Ehleringer 1994), el desierto cálido de Mojave (Yoder & Nowak 1999; Scholz et al. 2002), los ecosistemas sabanoides de África (Smith et al. 1999), Australia (Burgess et al. 1998; Burgess et al. 2000a; Burgess et al. 2001), y Sudamérica (Scholz et al. 2002; Moreira et al. 2003), las zonas mediterráneas de California (Millikin Ishikawa & Bledsoe 2000; Querejeta et al. 2003; Querejeta et al. 2007) y el nordeste de España (Peñuelas & Filella 2003; Filella & Peñuelas 2003). No obstante, la redistribución hidráulica tiene lugar también en ecosistemas mucho más templados como bosques costeros del Pacífico en Canadá, donde juega un papel muy importante en el balance hídrico (Brooks et al. 2002), bosques costeros atlánticos dominados por arces en Norteamérica (Dawson 1993), y praderas sobre substratos calcáreos en Europa (de Kroon et al. 1998). Aunque la redistribución hidráulica en zonas templadas y climas mediterráneos está relacionada con períodos relativamente secos, también tiene lugar cuando existen diferencias de humedad significativas entre capas de suelo durante periodos no tan secos. Estas condiciones de distinta humedad entre las capas del suelo se dan de forma frecuente en ambientes semi-áridos durante todo el año, ya que están sometidos a periodos de sequía cortos entre eventos de precipitación (Lazaro et al. 2001). Además, los ambientes semi-áridos se caracterizan por un largo período de estrés durante el cual las plantas están sometidas a una limitación crónica de agua (Pugnaire 1993). Esta limitación es particularmente acusada durante el periodo estival cuando las precipitaciones son mínimas y la temperatura y la radiación son más altas (Figura 1).

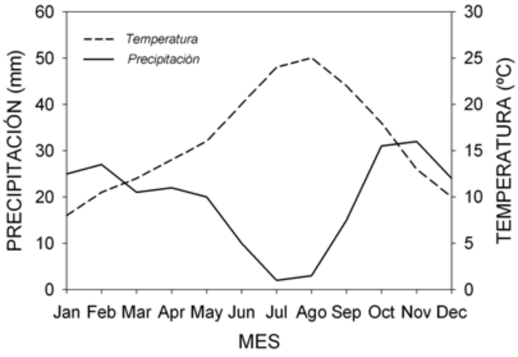

Fig 1. Precipitación y temperatura media mensual en el desierto de Tabernas (Almería, España, 37º 08´ N, 2º 22´ W, 490 m.s.n.m). La temperatura media anual es de 17.8 ºC y la precipitación media para el período 1967-1997 es de 232mm.

Objetivos

El objetivo fundamental de la tesis es a) profundizar en el estudio de los patrones y los mecanismos de redistribución hidráulica en el suelo y su dependencia de factores edáficos (textura, humedad del suelo…), así como su evolución estacional en ecosistemas semi-áridos y b) las posibles implicaciones ecofisiológicas para las especies de estos ecosistemas. Este trabajo se considera básico para el avance de la investigación sobre el uso eficiente del agua en especies de ecosistemas áridos, así como para elucidar las posibles implicaciones fisiológicas y ecológicas del fenómeno en ecosistemas semi-áridos. Para ello consideraremos dos líneas básicas de investigación:

1. Estudio de los patrones de redistribución hidráulica y dependencia de los principales factores ambientales (e.g. eventos de precipitación, baja presión de vapor) y de las propiedades del suelo

En general, el contenido en agua del suelo y el gradiente de potencial hídrico entre diferentes capas del suelo condiciona que exista una mayor o menor cantidad de redistribución hidráulica (Caldwell et al. 1998; Richards and Caldwell 1987). En ambientes semi-áridos Mediterráneos con un componente estacional caracterizado por una fuerte sequía estival, la variación en la disponibilidad de agua en capas superficiales se ve fuertemente condicionada por una mayor o menor cantidad de eventos de precipitación. En épocas húmedas (e.g. invierno) los potenciales hídricos del suelo son mayores que durante la época seca (e.g. verano), así la diferencia de potencial hídrico entre las capas profundas y superficiales del suelo, y por tanto el gradiente de potencial creado, será mayor durante las épocas de sequía (Kurz et al. 2006; Millikin Ishikawa and Bledsoe 2000; Scholz et al. 2008). Así pues, es de esperar que la redistribución hidráulica sea variable de forma estacional a lo largo del año. Diversos estudios en este campo han observado patrones estacionales en la redistribución hidráulica, observándose una mayor redistribución durante periodos secos cuando el gradiente de potencial es mayor entre capas del suelo (Millikin Ishikawa and Bledsoe 2000). Además, eventos puntuales de precipitación durante épocas secas pueden hacer que el potencial hídrico del suelo en capas superficiales aumente de forma temporal invirtiendo el gradiente de potencial y haciendo que se produzca redistribución hidráulica inversa (Burgess et al. 1998; Hultine et al. 2003). También otros factores como la transpiración nocturna (Dawson et al. 2007; Donovan et al. 2003) o una baja presión de vapor durante el día (e.g. días nublados) podrían provocar un efecto sobre la redistribución hidráulica al modificar los gradientes de potencial en el continuo suelo-planta-atmósfera (Sperry 2000). Una baja presión de vapor provocaría el cese de transpiración en la planta haciendo que la redistribución hidráulica se produzca de forma anómala durante el día (Espeleta et al. 2004; Williams et al. 1993). Por el contrario, la transpiración nocturna haría que la redistribución hidráulica se vea reducida en magnitud, del mismo modo que durante el día la transpiración inhibe el fenómeno y favorece la absorción de agua por las raíces (Snyder et al. 2008). Estas cuestiones se abordan en el Capítulo I donde se estudiaron los patrones estacionales de redistribución hidráulica en el arbusto *Retama sphaerocarpa*. En este capítulo también se vio la dependencia de la redistribución hidráulica de los potenciales hídricos del suelo y cómo a su vez, esta redistribución es dependiente de la transpiración de la planta.

Otros factores relacionados con el tipo de suelo donde crece la planta, como la textura y porosidad, también pueden afectar al contenido de humedad del suelo y a la disponibilidad de agua para esas plantas (Hillel 2004) . En diversos estudios se ha observado que la intensidad de la redistribución hidráulica estuvo negativamente relacionada con el contenido de arena del suelo (Hultine et al. 2005; Yoder and Nowak 1999). Al parecer, la redistribución hidráulica disminuye en suelos de textura gruesa y aumenta en suelos de textura más fina. En otro estudio llevado a cabo por Schenk et al. (2003), el efecto positivo que *Ambrosia dumosa* ejercía sobre las hierbas anuales vecinas, atribuido por ellos a un posible efecto de la elevación hidráulica, era más fuerte en suelos limosos que en suelos arenosos (Schenk y colab. 2003). Sin embargo, los datos sobre el papel que ejerce el tipo de suelo en la elevación hidráulica son demasiado incompletos y se necesita una investigación más detallada. En el Capítulo II se aborda esta cuestión con un experimento en el que se suprimió la transpiración en cinco especies de arbustos semi-áridos con el objetivo de estudiar los patrones de redistribución hidráulica y, a través de un modelo, establecer su dependencia en un rango amplio de texturas del suelo.

2. Implicaciones de la redistribución hidráulica sobre la fisiología y crecimiento de especies vegetales de ecosistemas semiáridos:

3.1 *Para la propia especie que realiza redistribución hidráulica*

Diversos mecanismos hacen que las plantas en medios áridos y semi-áridos utilicen el agua disponible de manera muy eficiente (Ehleringer et al. 1999). La redistribución hidráulica, entre otros, se ha propuesto como un mecanismo que puede ser decisivo tanto en el balance hídrico de ecosistemas enteros como para el uso del agua por cada planta de forma individual (Burgess et al. 1998; Emerman and Dawson 1996; Horton and Hart 1998; Jackson et al. 2000). Se ha sugerido que la redistribución hidráulica también puede tener implicaciones en otros procesos fisiológicos que ocurren en la planta, como el mantenimiento de las raíces finas (Caldwell *et al.* 1998), la absorción de nutrientes (Caldwell et al. 1998; Dawson 1996; Matzner and Richards 1996; McCulley et al. 2004) o la prevención del embolismo en raíces (Domec et al. 2004). Fuera de la planta, la redistribución hidráulica también actúa sobre el mantenimiento de las micorrizas en suelos muy secos (Querejeta et al. 2003; 2007). Sin embargo, a pesar de la importancia que ejerce sobre la propia planta elevadora, no existe un conocimiento profundo de los patrones y mecanismos de la redistribución hidráulica ni de muchas de sus implicaciones fisiológicas. En el Capítulo III, mediante un estudio de invernadero donde se suprimió de forma experimental la redistribución hidráuilca, se estudio cómo este fenómeno afecta al crecimiento de raíces dentro de parches de suelo ricos en nutrientes, aumentando así la absorción de estos nutrientes por parte de la planta levantadora. En el capítulo V se revisan de forma más detalla todos los efectos de la redistribución hidráulica sobre la parte subterránea de las especies que la realizan tanto desde un punto de vista fisiológico como en un aspecto más ecológico.

3.2 *Para especies que crezcan en la zona de influencia de especies levantadoras y que se ven afectadas por mecanismos de facilitación y competencia por agua con la planta levantadora.*

El agua levantada hidráulicamente también puede afectar a las interacciones entre la planta levantadora y las plantas que crecen en sus alrededores (Caldwell et al. 1998; Horton and Hart 1998). Las especies que crecen cerca de especies con acceso a agua profunda parecen verse beneficiadas por el agua levantada hidráulicamente, como así lo han demostrado numerosos estudios donde se observó que individuos que crecen cerca de plantas elevadoras tomaban el agua levantada, mejorando así su estado hídrico y su transpiración (Corak et al. 1987; Dawson 1993; Sekiya and Yano 2004). Recientemente, varios estudios han demostrado una transferencia directa de agua levantada hidráulicamente de plantas levantadoras a plántulas a través de redes micorrícicas del suelo (Egerton-Warburton et al. 2007; Schoonmaker et al. 2007; Teste and Simard 2008; Warren et al. 2008). En contraposición, Ludwig *et al.* (2004) descubrieron en *Acacia tortilis* y especies de herbáceas que crecían en su zona de influencia que el efecto de la competencia por el agua era mayor que los efectos positivos del agua levantada desde capas más profundas por esa especie. Además, el efecto facilitador puede ser distinto para diferentes especies que vivan cerca de la especie levantadora (Zou et al. 2005) o puede actuar en un periodo durante el cual el agua levantada no sea accesible para las plantas porque se produce fuera de su periodo de crecimiento (Millikin Ishikawa and Bledsoe 2000). Todos los estudios mencionados se han basado en medidas fisiológicas, el estudio hídrico de la planta o en estudios de crecimiento y biomasa, pero no en la supervivencia y establecimiento de plántulas en ecosistemas semiáridos. Por estas razones, más estudios son necesarios para evaluar el posible efecto de la redistribución hidráulica sobre la supervivencia y establecimiento de especies de herbáceas asociadas a planta levantadoras, así como en el crecimiento y biomasa en diferentes épocas del año. En los Capítulos IV y V se abordan estas cuestiones. En el capítulo IV se plantea un experimento de campo donde se estudia la supervivencia de un arbusto de escosistemas semiáridos (*Marrubium vulgare*) debajo de la copa de *Retama sphaerocarpa*. Diferentes tratamientos experimentales nos permitien evaluar el efecto de la redistribución hidráulica en el efecto facilitador de *Retama* sobre *Marrubium*. El capítulo V revisa las implicaciones de la redistribución hidráulica sobre especies que crecen bajo la influencia de una planta que realiza redistribución hidráulica evaluando las posibles implicaciones ecológicas de este fenómeno desde un punto de vista global.

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En los ecosistemas áridos y semi-aridos de la provincia de Almería se dan las condiciones idóneas para el fenómeno de redistribución hidráulica

Capítulo I

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*Levantamiento hidráulico: procesos del suelo y transpiración en el arbusto mediterráneo Retama sphaerocarpa (L.) Boiss (Fam. Leguminosae)**

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Capítulo I

HYDRAULIC LIFT: SOIL PROCESSES AND TRANSPIRATION IN THE MEDITERRANEAN LEGUMINOUS SHRUB *RETAMA SPHAEROCARP*A (L.) BOISS

Summary

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 one 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 -4MPa). HL amplitude was negatively affected by nocturnal transpiration, and HL patterns were recorded in all seasons and at water potentials ranging from -0.1 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, Ψ_s = Soil water potential

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 & 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 & 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 & 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 & 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 & Jhonson 1992; Caldwell & 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 3-4 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 (37º 108'N, 21º 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 ºC (Pugnaire & 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 forming 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 m^2 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, 50, 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, 50 and 80cm 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 & 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 to 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 two 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 minutes 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 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 6.0 (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 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 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.

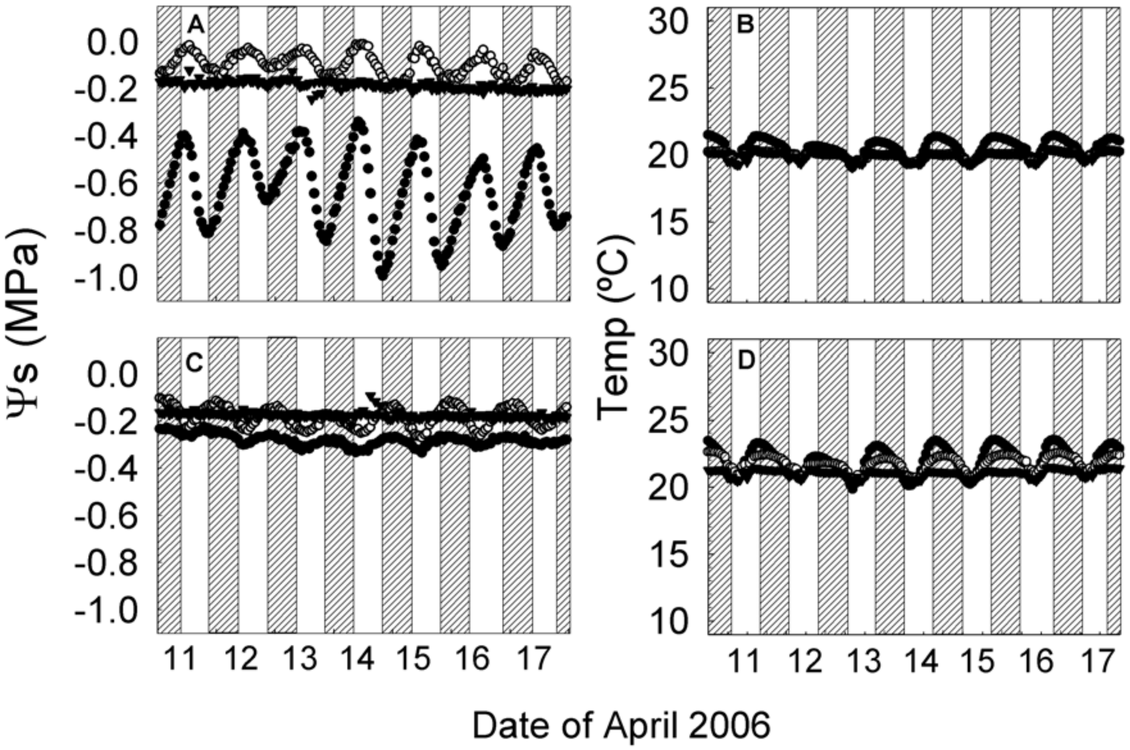

Fig. 1 Soil water potential and soil temperature diel cycles depicting HL under one *R. sphaerocarpa* representative individual (A,C) and in a control plot (B,D) during Spring 2006. Shaded bars represent nighttime. Solid and open circles represent 30 cm and 50 cm depth respectively; triangles represent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

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 & 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 four 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.

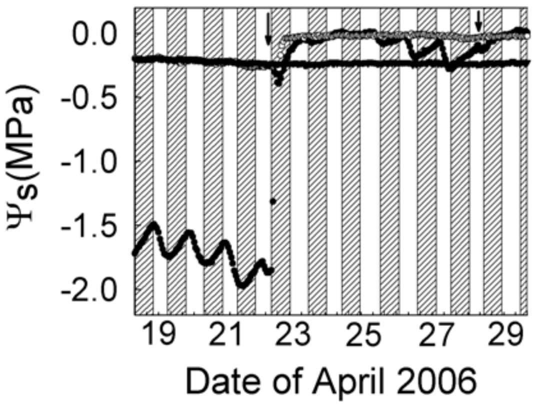

Fig. 2 Soil water potential cycles showing HL under one representative individual of *R.sphaerocarpa* during Spring 2006. Note the rapid cessation of HL cycles for three consecutive days at 30 cm due to the increase in soil water potential after a 27.6 mm and a 28 mm rain event took place on the 22nd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

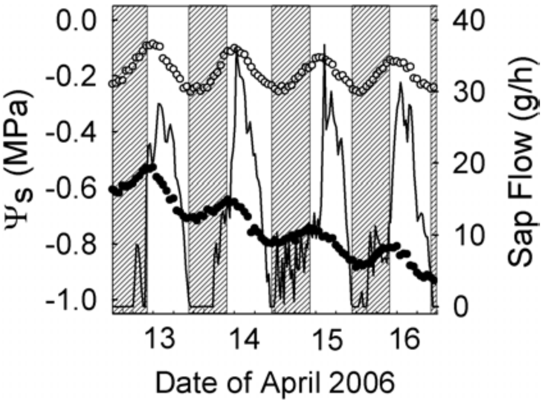

Fig. 3 HL cycles at 30 cm (solid circles) and 50 cm (open circles) under one representative individual of *R. sphaerocarpa* during spring 2006. Sap flow in one of the main stems is also represented (solid line). Nighttime sap flow occurred during some nights as shown by higher than zero values during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

The magnitude of the overnight increase in soil water potential due to HL ($\Delta\Psi_s$) at 30 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 30cm and in spring and winter 2007 at 50 cm, when mean soil water potentials ranged from -3 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.

Table. 1 Repeated measures ANOVA results for HL under *R. sphaerocarpa* shrubs at 30 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	0.0183	0.7012	0.613
	Error	8	0.0261		
50 cm	**Time (Season)**	3	0.0217	67.155	**<0.001**
	Error	6	0.0003		

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 & Bleby 2006; Hultine et al. 2003a; Hultine et al. 2004; Hultine et al. 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.

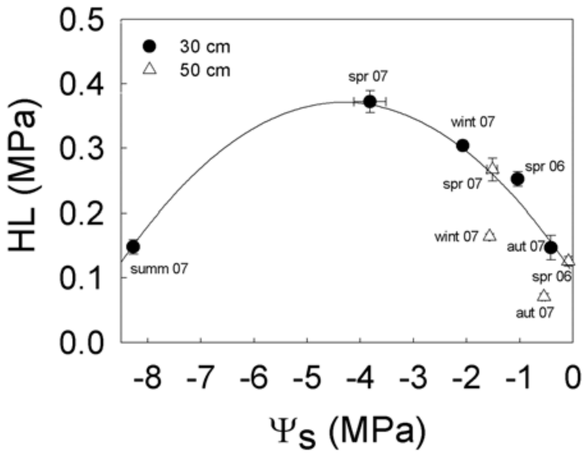

Fig. 4 HL amplitude ($\Delta\Psi_s$) as a function of soil water potential (Ψ_s) in the top 50 cm of soil under *R. sphaerocarpa* shrubs. Seasonal values are Mean ± 1 SE. Regression was significant at $P < 0.01$. (spr = spring; summ = summer; aut = autumn; wint = winter)

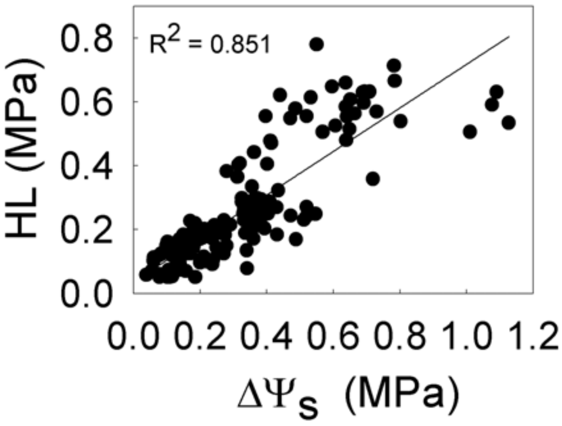

Fig. 5 Nighttime increases in soil water potential (HL, MPa) in 3 individuals of *R.sphaerocarpa* as a function of daytime changes in soil water potential ($\Delta\Psi_s$, MPa). Night increases in soil water potential (HL) were a function of previous day depletion of soil water potential ($\Delta\Psi_s$). Regression equation is HL (MPa) = $0.6825*\Delta\Psi_s+0.035$ Regression is significant at $P < 0.001$

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.sphaerocarpa* shrubs was ca 0.4 MPa (Fig. 2), which is similar to values previously reported in the literature.

Nighttime soil water potential increases of 0.4MPa 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 0.4MPa were also reported by Williams et al. (1993) in *Artemisia tridentata* individuals growing in the field. Smaller changes of 0.2MPa in dry soil (ca -4.5MPa) were reported for *Adesmia bedwellii* and *Proustia cuneifolia* (Muñoz et al. 2008) and in *Artemisia tridentata* (Richards & Caldwell 1987; Caldwell & 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 & 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 when shallow soil layers were extremely dry and thus create the conditions for HL even during extreme drought.

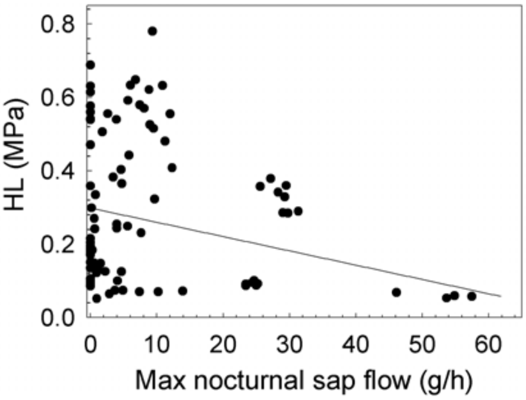

Fig. 6 HL (MPa) under 3 individuals of *R. sphaerocarpa* shrubs was negatively influenced by nocturnal transpiration measured as max nocturnal sap flow (g/h) in *R. sphaerocarpa* stems. Solid line indicates the trend of decreasing HL with increasing nighttime sap flow. $R^2 = 0.147$, regression was significant at $p < 0.001$

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 hypothesized 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 & Huang 1992; Vetterlein & 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 & 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 four 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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Capítulo II

*Estudio del levantamiento hidráulico a través de supresión de la transpiración en dos ecosistemas áridos: patrones y mecanismos de control**

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Capítulo II

HYDRAULIC LIFT THROUGH TRANSPIRATION SUPPRESSION IN SHRUBS FROM TWO ARID ECOSYSTEMS: PATTERNS AND CONTROL MECHANISMS

Summary

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 depends on plant physiology and soil properties. In this paper 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 at different depths under the shrubs was recorded. 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

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 confer them the ability to switch between shallow and deep water sources depending on availability (Canadell & Zedler 1995; Dawson & Pate 1996; Schenk & Jackson 2002). Deep roots may connect soil layers widely differing in 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 and termed “hydraulic lift (HL)” (Richards & Caldwell 1987). Burgess et al. (1998) used a more comprehensive term for the phenomenon, “hydraulic redistribution (HR)”, since it is now known that water moves also 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 & 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 happens also 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 makes hydraulic redistribution a widespread phenomenon that seems to be the rule rather than the exception in terrestrial ecosystems. Apart from its interest 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 community and ecosystem levels (Lee et al. 2005; Amenu & Kumar 2008; Nadezhdina et al. 2008; Scott et al. 2008). On the ecosystem scale, HL can modify seasonal microclimate by increasing transpiration during dry periods (Lee et al. 2005). On 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 the 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 roots function and mycorrhizal networks under dry conditions (Querejeta et al. 2003; Bauerle et al. 2008) or the prevention of air-induced embolism in roots (Domec et al. 2004) among others. Hydraulic redistribution has also been proposed as a mechanism buffering 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 decrease in soil water potential under *Pinus ponderosa* and *Pseudotsuga meinziesii* trees was faster when hydraulic redistribution was not operating. This buffering effect could play an important role under conditions of low transpiration demand, such as cloudy days or periods of low vapour pressure deficit, and could potentially recharge the upper soil layers through 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 & Richards 1989; William et al. 1993) but few have focused on the effect that suppressed transpiration exerted 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 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 morphology and function, our study was repeated in the spring of two different years (2005 and 2008) and in two different sites (Spain and Chile) both with dry Mediterranean-type climate but differing 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 would increase continuously until transpiration was restored; 2) the amount of hydraulically redistributed water would be highly dependent on soil texture, with coarse-textured soils being less conducive to HL than fine-textured soils; and 3) HL patterns would differ between sites with different soil texture and annual rainfall regimes.

Methods

Study sites and species

One of the study sites is located in Quebrada El Romeral in the Coquimbo region, north-central Chile (29º43'S - 71º14'W, 300 m elevation). The climate is arid Mediterranean with influence from coastal fog and a mean annual precipitation of 76.5 mm in the last 30 years (Squeo et al. 2006). Mean annual temperature is 14.5 ºC. The soil is from alluvial origin with a sandy texture mixed with stones and gravel. The vegetation is a coastal steppe formation with short sclerophyll shrubs covering 20-30% of soil surface (Olivares & 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 higher up the dominant species are *Haplopappus parvifolius* (DC.) A. Gray, *S. cumingii* and *P. revolutus*.

Another study site was located in the lower zone of the Rambla del Saltador, a dry valley in the southern slope of the Sierra de los Filabres range, Almería, SE Spain (37º08´N - 2º22'W, 630 m elevation). The climate is semi-arid Mediterranean with a mean annual precipitation of 250 mm (Haase et al. 1999). Mean annual temperature is 15.8 ºC. The soil is from alluvial origin with a loamy sand texture. The valley is on micaschist bedrock, where erosion 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 in the Quebrada El Romeral site were two drought-deciduous shrubs, *Flourensia thurifera* (Molina) DC. and *Senna* *cumingii* (Hook. & Arn.) H.S. Irwin et Barneby; and an evergreen shrub, *Pleocarphus revolutus* D. Don, all endemic to Chile. They all have dimorphic root systems and showed evidence of hydraulic lift (León & 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 with a dimorphic root system as well that reaches >1 m deep (I. Prieto, per. obs.).

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 h 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 of 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 in Rambla del Saltador (Spain). Each sensor was individually calibrated against KCl solutions of known molality (Brown & Bartos 1982). 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 inserted through the tube with the intention of leaving it as close as possible to the main root, where we expected 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 greater than ± 5 were discarded. Soil water potential was monitored before, during, and after the plants were covered.

Volumetric water content

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

(eqn. 1)
$$\theta_i = \theta_r + \frac{\theta_s - \theta_r}{\left[1 + \left|\alpha \Psi_i\right|^n\right]^m}$$

Where

θ_i = volumetric water content (cm^3/cm^3) at water potential i

α and n were 0.075 and 1.89 respectively for sandy soils

m = 1-1/n

θ_r = residual volumetric water content (cm^3/cm^3)

θ_s = saturated volumetric water content (cm^3/cm^3)

Ψ_i = soil water potential (MPa)

In Rambla Honda, the volumetric water

content was calculated through 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.

(eqn.2) $$\theta_i = 9.6793 \times e^{\left(89.4764/(\Psi i+59.1755)\right)}$$

Where:

θ_i = volumetric water content (cm^3/cm^3) at water potential i

Ψ_i = soil water potential (MPa)

Hydraulic lift model

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:

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

Where:

$\Psi_{s(t)}$ = soil water potential at time t (day)

Ψ_0 = soil water potential at t = 0.5 (midday)

$\Delta\Psi$ = nocturnal increase in water potential on day t

α = slope of the straight line obtained from plotting mean daily soil water potentials.

t = time (day)

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 *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 eqn. 3 to calculate the decrease in soil water potential had the plants been left uncovered (termed as *expected potential* hereafter, Ψ_{est}).

Using the equations in Fig. 3 we calculated the difference between 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 & 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 factor, and a one-way MANOVA with $\Delta\Psi$ and $\Delta\theta$ as dependent variables and “site” as 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 variances 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.

Table 1. Soil parameters for the Van Genuchten equation for seven different soil textures. Standard Errors (SE) were calculated from the standard deviation (SD) in Hodnett & Tomasella (2002) and n=497. α and n are shape parameters of 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

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

Modified from Hodnett & Tomassella (2002)

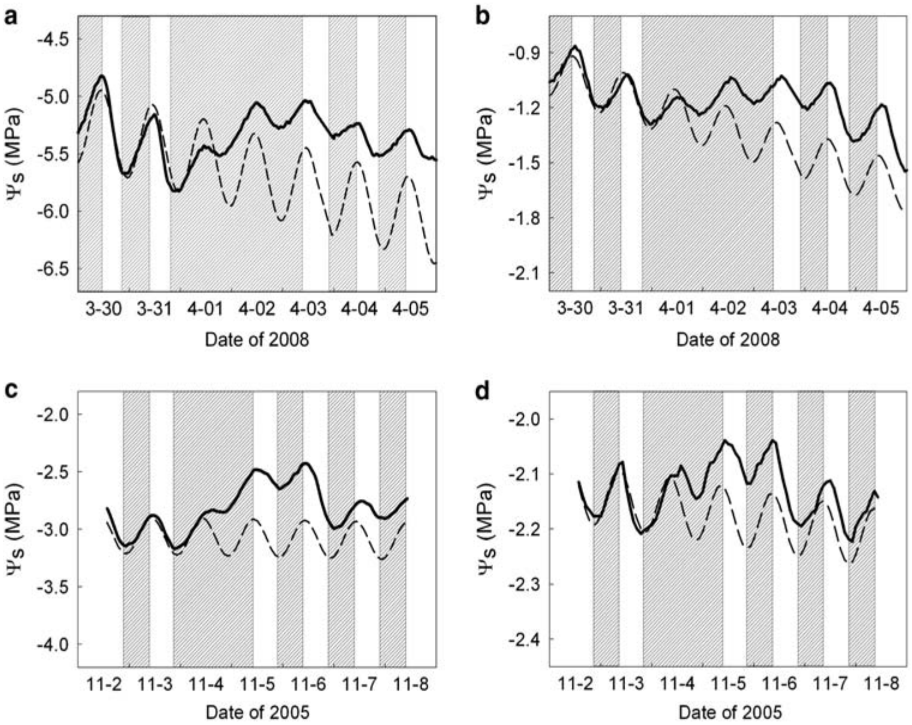

Fig. 1 Soil water potential (Ψ_s) measured at 30 cm depth under one representative individual of *Retama sphaerocarpa* (a) and *Artemisia barrelieri* (b) in Spain and at 40 cm depth under one representative individual of *Flourensia thurifera* (c) and *Senna cumingii* (d) in Chile. Solid lines represent 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 while plants were covered. All these plants were subjected to transpiration suppression (thick grey bars). Note the different scales on the y-axis

Results

During the days prior to treatment application we found the 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 of *P. revolutus* and *R. sphaerocarpa* respectively.

Table 2. Rooting depth data for the five species included in the study. N.a = not available

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

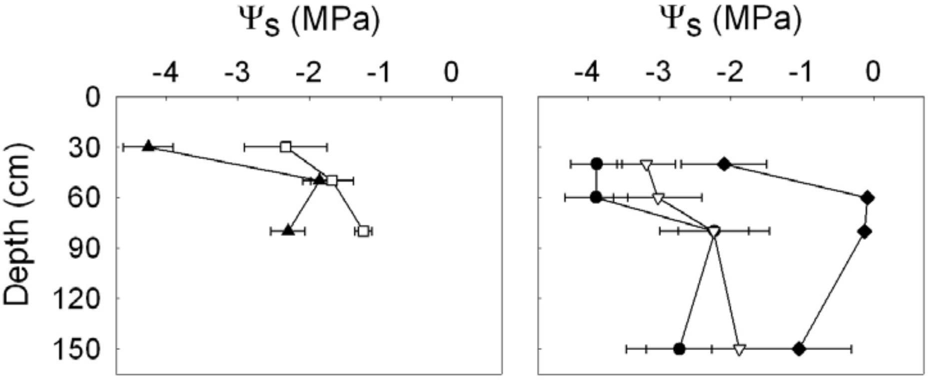

Fig. 2 Soil water potential (Ψ_s) measured within the rhizosphere under individuals of the species under study one day before the transpiration suppression treatment took place (n=4 except for *S. cumingii* n=3 at 80 cm and n=2 at 150 cm and *P. revolutus* n=2 at 40 cm and n=1 for *P. revolutus* at 60,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

Table 3. Soil water potential and volumetric water content at 30 cm and 40 cm in Spain and Chile respectively, before transpiration suppression (Ψ_a; θ_a) and 24 h after transpiration suppression (Ψ_{obs} ; θ_{obs}). Estimated water potential was calculated from our model using eqn 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 eqn. 1 and eqn. 2 for Chile and Spain respectively (see material and 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 (Ψ_{obs} - Ψ_{est} and θ_{obs} - θ_{est}) indicates water was released into the soil. Data are mean ± 1 SE, n = 4 except for *P. revolutus* (n = 2) and *A. barrelieri* (n = 1)

Species	**Site**	**Ψ_a (MPa)**	**Ψ_{obs} (MPa)**	**Ψ_{est} (MPa)**	**Ψ_{obs} - Ψ_{est} (MPa)**	**θ_a (cm^3/cm^3)**	**θ_{obs} (cm^3/cm^3)**	**θ_{est} (cm^3/cm^3)**	**θ_{obs}- θ_{est} (cm^3/cm^3)**
F. thurifera	Chile	-4.11 (± 0.33)	-3.90 (± 0.38)	-4.13 (± 0.33)	0.23 (± 0.055)	2.480 x 10^{-3} (± 2.00 x 10^{-4})	2.590 x 10^{-3} (± 2.57 x 10^{-4})	2.439 x 10^{-3} (± 1.93 x 10^{-4})	1.51 x 10^{-4} (± 1.62 x 10^{-5})
P. revolutus	Chile	-2.12 (± 0.33)	-2.12 (± 0.49)	-2.25 (± 0.57)	0.13 (± 0.086)	4.643 x 10^{-3} (± 1.14 x 10^{-3})	4.547 x 10^{-3} (± 9.37 x 10^{-4})	4.357 x 10^{-3} (± 9.95 x 10^{-4})	1.90 x 10^{-4} (± 5.85 x 10^{-5})
S. cumingii	Chile	-3.24 (± 0.54)	-3.13 (± 0.58)	-3.32 (± 0.56)	0.22 (± 0.080)	3.193 x 10^{-3} (± 4.62 x 10^{-4})	3.333 x 10^{-3} (± 4.97 x 10^{-4})	3.159 x 10^{-3} (± 4.82 x 10^{-4})	1.74 x 10^{-4} (± 1.62 x 10^{-5})
R. sphaerocarpa	Spain	-4.49 (± 0.45)	-4.41 (± 0.70)	-4.73 (± 0.74)	0.32 (± 0.092)	9.876 x 10^{-2} (± 1.7 x10^{-4})	9.878 x 10^{-2} (± 1.5 x10^{-4})	9.866 x 10^{-2} (± 1.6 x10^{-4})	1.24 x 10^{-4} (± 2.6 x 10^{-5})
A. barrelieri	Spain	-1.29	-1.23	-1.47	0.24	10.3427 x 10^{-2}	10.3751 x 10^{-2}	10.2623 x 10^{-2}	1.13 x 10^{-3}

These values were always greater than 0.01 MPa and were thus considered to be indicative of HL (Millikin-Ishikawa & Bledsoe 2000). Only in one *A. barrelieri* individual diel patterns in soil water potential agreed with HL patterns but in the other three individuals, such cycles were not detected. This suggests that the species was able to perform HL but the lack of responses in three plants was rather 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 these cycles was greatest at 30 cm (Spain) or 40 cm depth (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 of 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 have active fine roots in the upper 60-100 cm of soil and deep roots, either tap or sinker roots, that can easily grow below 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 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 (±0.092) MPa in *R. sphaerocarpa* to 0.13 (±0.086) MPa in *P. revolutus*. This rise in soil water potential resulted in an increase of volumetric water content under the shrubs which was maximum under one individual of *A. barrelieri* with a total of 1.13 * 10^{-3} cm^3/cm^3 of water lifted and minimum under *R. sphaerocarpa* with a mean total of 1.24 * 10^{-4} (±2.6 * 10^{-5}) cm^3/cm^3 (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 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 eqn. 3 and measured values were very close (R^2=0.998, p<0.001). This suggests that the equation developed to reproduce HL patterns (eqn. 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, $F_{1,40}$=8.273,

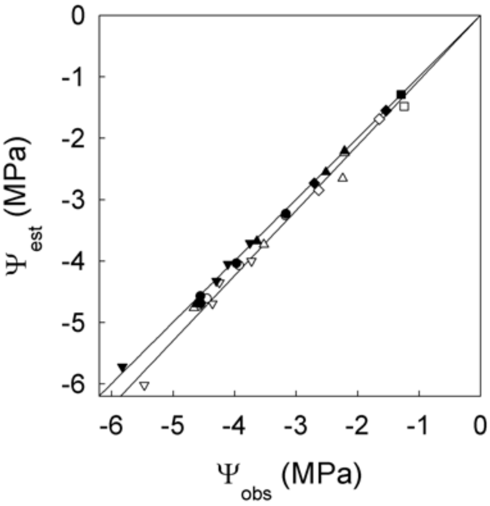

Fig. 3 Estimated vs. observed soil water potentials measured in the rhizosphere of five shrub species in Chile and Spain before (solid symbols) and after (open symbols) suppressed transpiration. Regression lines are shown. Regression equations were Ψ_{est}=0.9993* Ψ_{obs} (r^2=0.998; $P<0.001$) and Ψ_{est}=1.0597* Ψ_{obs} (r^2=0.989; $P<0.001$) respectively. Legend as in Fig. 2

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 ($\Delta\theta_s$) was 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 5 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 rhizosphere of these shrubs were indicative of their ability to lift water from deep soil layers and release it into upper, dry soil layers at nighttime resulting in an increase in soil water potential. We cannot provide isotopic evidence of deep 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 source for hydraulically lifted water into shallow layers during dark periods.

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

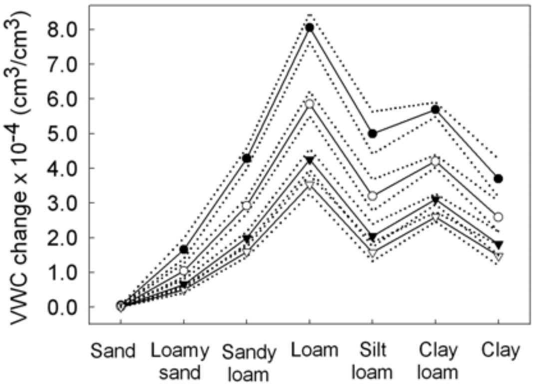

Fig. 4 Soil volumetric water content change (VWC) due to HL for seven soil types differing in texture calculated at four different soil water potentials, -1 MPa (solid circle, ●), -2 MPa (open circles, ○), -4 MPa (solid triangles, ▼) and -6 MPa (open triangles ▽). Values were calculated from the regression equations in Fig. 3 and using van Genuchten's (1980) soil parameter values for the different textures (see Methods section and Table 3). Dotted lines represent 95% confidence intervals for the curves

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 that could then enhance transpiration rates (Caldwell & 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, thus rejecting our hypothesis that differences between sites would modify HL patterns and its magnitude. We would expect differences in HL as soil texture varied between sites but results from our model showed a similar magnitude of HL between 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 in 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 on a drying cycle. The model allowed for comparison of soil water potential changes 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 which 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

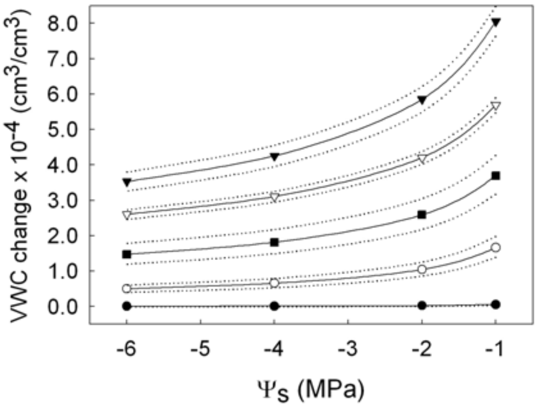

Fig. 5 Soil volumetric water content change due to HL in a range of soil water potentials for five soil types differing in texture, sand (solid circle, ●), loamy sand (open circle, ○), loam (solid triangle, ▼), clay loam (open triangles ▽) and clay (solid square, ■). Values were calculated from the regression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

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 & Tomassella 2002). This suggests that water is lost rapidly while causing only a small decrease in water potential. In addition, loamy soils can also store water in a form more available for plants than finer-textured soils (Bristow 1984), which may allow for a 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 & 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 high water amounts (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 & Nowak, 1999; Hultine et al. 2006; Siqueira et al. 2008; Wang et al. 2009). The relationship with texture becomes non-linear in more clayish soil types that have intermediate properties between sandy and loamy soils regarding HL. Yoder & 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 the 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 could transport from deep, wet soils to shallow, dry soil layers, which strongly depends on the type of soil they are growing on (Fig. 5).

Soil texture can also influence plant traits such as root morphology (Sperry & 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 & Nowak 1999; Aanderud & Richards 2009). Wang et al. (2009) reported greater HL in the rhizosphere 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 & 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 might be an oversimplification of the HL phenomenon and, as stated above, other factors might influence HL patterns or magnitudes, the consistency between our modelled results and previous reports makes us believe our approach is useful to understand 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 non-linear relationship between soil water potential and soil water content which in our model resulted in a lower HL magnitude at low water potentials (see Figs. 4 and 5). The large gradients in soil water potential during drought resulted in smaller amounts of water released into the top soil layers under *R. sphaerocarpa* (Prieto et al. 2010). Nonetheless, factors such as a decrease in root hydraulic conductivity or 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 & 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 this species had 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 during short periods (48-72 h). In *R. sphaerocarpa* this phenomenon extended 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 upper soil layers was generally low. HL only accounted for 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 survival of associated mycorrhiza (Querejeta et al. 2007; 2009) or lowering root xylem cavitation (Domec et al. 2004). In sandy soils this phenomenon can be of great importance as shrubs usually experience a higher vulnerability to xylem cavitation (Sperry & Hacke 2002). In leguminous shrub species HL could also help maintain associated N-fixing bacteria (Athar et al. 1997; Swaine et al. 2007) through mitigation of decreasing soil water potentials during drought (Meinzer et al. 2004).

In summary, we found a new species performing HL in arid systems. We also accurately simulated HL patterns with a simple model that can be a useful tool for studying HL effects at the community level; importantly enough, we found a correlation between soil texture and the volume of water redistributed and that HL was more efficient when 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 being released into the soil.

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Capitulo III

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*El levantamiento hidráulico promueve la colonización selectiva de parches de suelo ricos en nutrientes en una especie de ecosistemas semi-áridos**

*Enviado como: Prieto I, Armas C, Pugnaire FI (2010) Hydraulic lift promotes selective root foraging in nutrient-rich soil patches in a semi-arid shrub species

Capítulo III

HYDRAULIC LIFT PROMOTES SELECTIVE ROOT FORAGING IN NUTRIENT-RICH SOIL PATCHES IN A SEMI-ARID SHRUB SPECIES

Summary

It has been shown that hydraulic lift (HL), or the passive movement of water from deep wet to shallow soil layers, can improve root survival in dry soils by providing an extra source of moisture to shallow roots. This extra moisture may also enhance plant nutrient uptake, although evidence in this direction is scarce. Whether HL promotes the selective placement of roots in nutrient-rich soil patches - root foraging - enhancing nutrient uptake in dry soils remains unknown. We tested whether HL enhanced root colonization into resource-rich patches and if this process contributed to nutrient uptake. We addressed these points in a shrub species characteristic of a semi-arid ecosystem and, using a split-pot design, separated its root system into two compartments –a lower, well watered and an upper, drier one. Half the shrubs grew under natural light conditions and were allowed to perform HL, whereas the other half had HL prevented by using continuous illumination at night. Resource-rich (organic matter enriched in ^{15}N and P) and resource-poor soil patches were inserted in the upper compartments after a drought treatment was imposed. We found that soil moisture in the upper compartments and in soil patches was greater in shrubs that performed HL than in shrubs that did not. Root foraging precision and plant nitrogen assimilation was also greater in shrubs that performed HL, suggesting that HL favoured the selective placement of roots in nutrient-rich patches as well as nutrient uptake under drought conditions. To our knowledge, this is the first study linking HL with root foraging and nutrient uptake, a process that could secure nutrient uptake and maintain plant performance during drought periods.

Introduction

Plants in arid ecosystems tend to be deep rooted (Canadell *et al.*, 1996, Schenk & Jackson, 2002) and hence roots span and explore a wide volume of soil connecting layers with very different moisture. Under these conditions and in periods of low transpirational demand (e.g. at nighttime) water can move passively through the root system driven by water potential gradients. Some of this water is shed into shallow soil moistening dry layers, a phenomenon that is termed hydraulic lift (HL, Richards & Caldwell, 1987).

The process of HL has been extensively addressed (Caldwell, Dawson & Richards, 1998, Horton & Hart, 1998, Jackson, Sperry & Dawson, 2000, Ryel 2004) mostly focusing on its potential benefits for both the lifting plant (Ryel *et al.*, 2002, Caldwell & Richards, 1989) and its neighbors (Zou *et al.*, 2005, Dawson, 1993). Most of these benefits come from the extra water supplied overnight that increases water availability in shallow soil layers, increasing whole plant transpiration rates and carbon gain the next day (Dawson, 1997, Ryel *et al.*, 2002, Caldwell *et al.*, 1989). HL has also benefits for belowground plant parts and rhizosphere, such as i) hydraulic redistribution (HR) from root parts experiencing high water potentials to drier root parts minimizes the hazardous effect of soil drying and increases root survival (Bauerle *et al.*, 2008a); ii) internal HR fills up xylem vessels reducing root embolism, thus maintaining greater hydraulic conductivity (Domec, Warren & Meinzer, 2004); iii) HL can maintain roots hydrated whenever they experience low soil water potentials (Valenzuela-Estrada *et al.*, 2009), and iv) some of the water transported to shallow roots can be passively transferred to root symbionts (e.g. arbuscular mycorrhizal fungi) increasing their survival during drought periods (Warren *et al.*, 2008, Egerton-Warburton, Querejeta & Allen, 2007, Querejeta, Egerton-Warburton & Allen, 2003). To our knowledge, only one study have dealt with issues directly linking fine root survival with HL processes (Bauerle *et al.*, 2008a) and it did not include its potential influence on nutrient uptake or mediated responses to nutrient heterogeneity. All the above-mentioned processes have been hypothesized to increase root growth rates in dry soils and have been proposed to indirectly facilitate nutrient uptake from shallow soil layers (Liste & White, 2008, Caldwell *et al.*, 1998) where nutrients mostly accumulate (Jobbagy & Jackson, 2001). However, conclusive evidence in this field is still scarce (but see Armas *et al.* unpublished).

Nutrients in soil are not homogenously distributed, and rich-soil patches co-occur with nutrient and/or water-depleted soil patches (Jackson & Caldwell, 1993). Typically, plants show a plastic response to soil nutrient heterogeneity and roots proliferate in regions where nutrients and water are most available (Bauerle *et al.*, 2008b, Jackson & Caldwell, 1989, Hutchings & de Kroon, 1994) avoiding regions where they are in short supply (Drew, 1975). However, the majority of the studies that analyzed these plastic responses to nutrient heterogeneity, or root foraging behavior (de Kroon & Hutchings, 1995), have been carried out under ample water conditions (Hodge, 2010 for a review), and evidence of heterogeneously distributed nutrients in soils that readily dry out are scarce (but see de Kroon *et al.*, 1998). In this case, HL can at least theoretically promote root growth into nutrient-rich soil patches by hydrating fine roots, by increasing soil humidity and the availability of soil nutrients for the plants and, overall, by enhancing plant nutrient uptake from soil patches moistened via HL.

To date, most studies linking HL with nutrient uptake have been carried out with grass species (de Kroon *et al.*, 1998, Huang, 1999, Valizadeh, Rengel & Rate, 2003, Rose *et al.*, 2008, Wang *et al.*, 2009) while the few that used trees or shrub species either lacked true controls with HL suppressed (Leffler *et al.*, 2004, Hawkins *et al.*, 2009), used liquid nutrient solutions that can easily be absorbed by plants despite soil humidity condition (Matzner & Richards, 1996, Caldwell & Manwaring, 1994, Snyder *et al.*, 2008, Leffler *et al.*, 2004) or did not directly measure nutrient uptake (Dawson, 1997).

However, current research in this field is advancing, and recently, Aanderud & Richards (2009) demonstrated that the daily soil drying-rewetting cycles due to HL might enhance organic matter decomposition under dry soil conditions. They hypothesized that greater decomposition rates could promote greater nutrient availability for plants although they did not directly measure it. One step further, Armas *et al.* (unpublished) have recently demonstrated that HL not only promotes organic nitrogen mineralization under drying conditions but that HL makes soil nitrogen available for plants and plants can take up this N. However, it still remains unknown whether HL promotes root colonization in nutrient rich soil patches, and by enhancing both root growth and soil water conditions in rich patches it aids plant nutrient uptake.

In this study, we hypothesized that HL supports root growth and foraging in resource-rich soil patches under dry soil conditions. We tested these hypotheses in a greenhouse experiment using a split-pot design with discrete nutrient-rich (organic matter enriched in ^{15}N and P, NR patches) and control (C) soil patches. The pots included a deep wet and shallow dry soil layers kept hydraulically apart by an air barrier that prevented water flow between soil layers. The target species was *Retama sphaerocarpa* (L.) Boiss, a phreatophytic, leguminous shrub with the ability to perform hydraulic lift (Prieto, Kikvidze & Pugnaire, 2010, Prieto *et al.*, 2010). After ten weeks we analyzed root growth in the discrete soil patches, plant N uptake from the nutrient rich patches and determined the occurrence of hydraulic lift.

We predicted that i) plants performing HL would have greater root growth in response to nutrient addition (NR patches) than those plants where HL was prevented by nighttime illumination; and that ii) a greater root colonization of NR patches would lead to increased nutrient uptake.

Methods

Soils

Soil was collected between 10-30 cm depth from a dry river bed in Almería province, SE Spain (37º 08'N, 2º 22' W, 630 m altitude). They were eutric fluvisols and had 50% of coarse sand, 36% fine sand, 10 % silt and 2.5% clay content. Soil had 0.77% of organic matter, with 0.14 % total N, 0.064 mol kg^{-1} Ca, 0.0061 mol kg^{-1} Mg, 0.0017 mol kg^{-1} Na and 0.0006 mol kg^{-1} K. Cation exchange capacity was low (0.0232 mol kg^{-1}) due to its low clay and silt content (Puigdefábregas *et al.*, 1996). Soil was air-dried and sieved (2 mm mesh size) to eliminate the coarser fraction and thoroughly mixed with type III vermiculite at 2:1 v/v (Verlite®, Vermiculita y Derivados SL, Gijón, Spain). The mix was used as soil substrate for the mesocosms split-pots.

Plant material and mesocosm establishment

Retama sphaerocarpa (L.) *Boiss* seeds were sown in potting soil under laboratory conditions at 25ºC and 12-hour light cycle in February 2006. Four weeks after emergence seedlings were transplanted to the experimental mesocosms – split-pots- and grown for three years until beginning of the experiment on May 2009. Mesocosms consisted of two PVC pots 23 cm diameter x 21cm height placed vertically one on top of the other. Both pots were connected through a 2cm diameter bottom opening in the upper pot ensuring root penetration and growth into the lower compartment. One week before the experiment started, we confirmed that all shrubs had roots colonizing the lower compartment. Upper pots were then fixed using scaffolding and the upper three centimetres of the lower pot were cut. The soil between pots was washed off creating an air barrier between upper and lower pots that prevented water flow between compartments. Exposed woody roots were protected with a fine layer of vaseline to avoid root damage.

When treatments started, water was withheld in all upper compartments of mesocosms whereas bottom compartments were maintained at field capacity throughout the experiment. Half the shrubs were subjected to 22h light + 2h dark period cycles in order to prevent hydraulic lift (non-hydraulic lift, NHL hereafter), whereas the other shrubs grew under natural conditions, with approximately 12h light + 12 dark cycles (hydraulic lift allowed, HL hereafter). Each treatment had a control; pots with the same soil but without shrubs and subjected to the same light treatments (n=3). Four 18W Grolux® fluorescent tubes (Osram Sylvania Inc.) and two 150W CFL Phillips Agrolite® light bulbs supplemented a total of 400 μmol m^2 s^{-1} and were daily switched on two hours after dusk (9 p.m. solar time) until dawn (5 a.m. solar time) in order to achieve the 22 hour light cycle. The beginning and end of the light cycle was adjusted as the experiment progressed to keep the 22h light 2h dark period constant throughout the experiment.

Labeled organic matter preparation and soil cores

Faba bean (*Vicia faba* L.) seeds were sown (3 seeds per pot) in April 2008 in pots 14cm diameter x 11cm height filled with sterile riverbed sand. After emergence of seedlings each pot was watered daily with tap water for 10 weeks except twice a week when pots were watered with 100 ml of a Hoagland's solution supplemented with $^{15}NH_4{}^{15}NO_3$ (800 mg/ml) and KH_2PO_4 (2.5 mM). Plants were harvested ten weeks later and leaves separated from stems. Leaves were then oven dried at 70ºC for 72h and finely ground and homogenized with a grinder. The resulting dry organic matter (^{15}N-P-OM) had a δ^{15}N value of ≈ 9000 ‰, equivalent to 3.5 atom %, and with 0.23 % of total P. This organic matter was then used to create discrete nutrient rich cores (NR patches, hereafter) of 18 cm^3 in volume by thoroughly mixing 1g of the enriched OM with 19 g of original soil (sieved through 2 mm mesh) and placing the resulting mixture within a plastic cylinder 60 mm height x 20 mm diameter. The cylinder wall was meshed with 5 x 3 mm holes that allowed root colonization into the patches. Control cores were created using the same procedure but the cylinder was filled with 20 g of sieved soil (thus, they were nutrient-poor soils, C patches hereafter).

One week after water was withheld in upper compartments and artificial light was supplemented, NR and C patches were inserted into the upper soil compartment at 10 cm depth; within each pot, two NR and two C patches were inserted in opposite directions with a cross-like design and at a middle distance between the shrub stem and the pot edge.

Irrigation with deuterium-labeled water

Nine weeks after treatments started 500 ml of deuterium-labeled water were added to the lower compartments. Labeled water was applied placing the lower pots inside a small bucket that contained the labeled water until all water was taken up by plants (aprox. four days). The buckets were covered with an aluminum foil to avoid over-heating and evaporation of labeled water that would lead to isotopic fractionation before root water uptake and redistribution. Deuterium-labeled water ($\delta D \approx 5000$ ‰) contained 0.78 ml of pure D_2O (99.8% deuterium enrichment, Sigma Chemical Co.) per liter of tap water.

Physiological measurements

Prior to the end of the experiment we assessed the physiological status of shrubs. Early in the morning, between 6-8 am solar time, we measured net photosynthetic rate (A) and stomatal conductance to water vapor (g_s) on mature well-developed green cladodes. Measurements were taken with an infrared gas analyzer (Li-COR 6400, Li-COR Biosciences Inc. Lincoln, NE, USA) under ambient CO_2 concentrations. Measurements were expressed on a leaf area basis. Maximum photochemical efficiency of photosystem II (Fv/Fm) was measured at dawn with a portable fluorimeter (PEA, Hansatech, Kings Lynn, UK) in cladodes previously dark-adapted for 30 min. Plant water potential (Ψ_p) was measured with a Scholander pressure bomb (SKPM 1400, Skye Instruments Ltd., Llandrindod Wells, UK) during the period when shrubs in both treatments were still in the dark.

Harvest, sampling and laboratory procedures

Ten weeks after water was withheld, at the end of the experiment, the NR and C soil patches were collected and plants were harvested. We separated aboveground tissues, fine (<2 mm) and coarse (>2 mm) roots from upper- and lower-compartments into different samples that were oven-dried at 70ºC for 72h and weighed separately.

We randomly selected 6-8 cladodes per plant (≈2-3 g) and 2-3 g of fine roots (<1 mm diameter) from the lower compartments, finely ground and analyzed them for $\delta^{15}N$. Cladodes were also analyzed for total N, P and C. Some cladode samples were also collected from five random shrubs prior to the beginning of the experiment in order to determine their $\delta^{15}N$ content.

NR and C soil patches, as well as bulk soil samples were carefully excavated, placed in plastic vials and immediately weighed for gravimetric water content determination (WC) and deuterium isotopic analyses. Then, samples were oven dried at 70ºC for 72h and weighed again. Soil gravimetric water content (%) was obtained as the weight difference (g) between wet and dry soil per unit dry soil (g). Subsamples of 1 g of soil were finely ground and homogenized using a mortar, and the $\delta^{15}N$ composition was then determined. Previously, roots had been cleaned, oven dried and weighed to obtain root density per patch ($g_{roots}/20\ g_{soil}$).

Root foraging was determined with the RII index (Armas, Ordiales & Pugnaire, 2004) following Maestre & Reynolds (2006). The index is calculated as $(RB_{NR} - RB_C)/(RB_{NR} + RB_C)$; where RB_{NR} is the root biomass in NR patches and RB_C is the root biomass in C patches. The index ranges from -1 to 1 with positive values indicating greater placement of roots into NR patches and hence increasing precision of root foraging, whereas negative values indicated the opposite.

Water for hydrogen isotope analysis was extracted from bulk soil samples collected at a depth of 10-15 cm in the upper compartments using a cryogenic vacuum distillation line (Ehleringer & Osmond, 1989). Both deuterium (*δD*) and $\delta^{15}N$ analyses were conducted at the Stable Isotope Facility, University of California, Davis. Deuterium content was determined using a Laser-Absorption Spectroscopy technique (LGR DLT-100 water analyzer, Los Gatos Research, Inc., Mountain View, CA, USA), whereas $\delta^{15}N$ content was determined with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Analytical precision was <0.8‰ for deuterium and ^{15}N analyses. Values are expressed in Delta notation and referred to the Vienna Standard Mean Ocean Water (V-SMOW) for deuterium and the Atmospheric Air Standard value for ^{15}N. Total N, P and C analyses were conducted at the Servicio de Ionómica department at the Centro de Edafología Aplicada del Segura (CEBAS) in Murcia (Spain). Total C and N content were determined using a Flash^{TM} EA 1112 CHN analyzer (Thermo Finningan, Italy) and total P content was determined using an Iris Intrepid II XDL analyzer (Thermo Fisher Scientific Inc. Waltham, MA, USA).

Statistical analyses

Differences in cladode, root or soil ^{15}N content, cladode nutrient content, above- and belowground biomass, RII, gravimetric soil water content, soil deuterium content and plant physiological responses were tested using one-way ANOVA. Differences in soil patches root biomass and soil patches gravimetric water content were analyzed with a factorial one-way ANOVA, with “treatment” and “patch” as independent factors. The average value from the two NR and two C patches was calculated within each plant and used as a single replicate. Data were log-transformed to ensure homostedasticity when necessary. Post-hoc differences were analyzed using Fishers´ LSD test. Pearson’s correlation analyses were performed across soil and plant variables.

All statistical analyses were performed using SPSS v.17.0 (SPSS Inc., Chicago, IL, USA). Data results throughout the text, tables and figures are presented as mean ± 1 SE.

Results

Soil moisture and isotope analysis

At the end of the experiment, soil gravimetric water content (WC) was low after ten weeks of imposed drought (less than 1% w/w), but there were significant differences among treatments (Table 1, one-way ANOVA $F_{3,9}$=12.719, *P*=0.001). WC in the HL treatment was significantly greater than that of its no-plant control (S12) and significantly greater that in pots where hydraulic lift was suppressed (NHL). Soil moisture in the latter treatment was marginally different from its no-plant control (S22) and did not differ from the no-plant control under 12 h light cycle (S12) (Fishers’ LSD test, *P*>0.30).

Table 1. Gravimetric water content (WC), deuterium content (*δD*) and ^{15}N in NR patches (Soil ^{15}N) in soil samples collected at the end of the experiment. Data are mean ± 1 SE (n=3 except for NHL where n=4). Different letters in a row show significant differences between treatments (*P*<0.05).

	HL	**NHL**	**S12**	**S22**
WC (%)	0.89 ± 0.05^{a}	0.60 ± 0.05^{b}	0.57 ± 0.04^{b}	0.48 ± 0.03^{b}
***δD* (‰)**	44.9 ± 7.16^{a}	-11.8 ± 7.80^{b}	-	-
Soil ^{15}N x 10^{3} (‰)	6.18 ± 0.21^{a}	6.13 ± 0.04^{a}	-	-

These results suggest 1) that evaporation rates from S12 and S22 were similar, despite being under different light regimes, and 2) although plants in the NHL treatment (i.e., under 22 h light cycles) transpired 10 h more than shrubs in the HL treatment (under 12 h light cycles) NHL plants could not take up water from the dry upper compartments at least by the end of the experiment, as WC in upper soils in both NHL and S22 treatments were similar. Likely NHL shrubs relied mostly on the bottom compartments to take up this water.

Deuterium content (*δD*) in soils supported the above results and provided evidence of HL. Soil water collected from upper compartments in the HL treatment was significantly richer in deuterium than upper compartments in the NHL treatment (Table 1). At the end of the experiment and across treatments, *δD* in soils from upper compartments was linearly and positively correlated to WC (Table 2).

Table 2. Pearson's correlation (r^2) coefficients for deuterium in soil water (*δD*) and gravimetric soil water content (WC) in samples collected from upper compartments, soil water content in NR soil patches (NR-WC), root foraging precision (RII) and ^{15}N, total nitrogen (N) and total phosphorus (P) content in shrub cladodes. All samples were collected at the end of the experiment (n=9)

	δD	**WC**	**NR-WC**	**RII**	**Cladode ^{15}N**	**Cladode N**
***δD* (‰)**	-					
Soil water content – WC (%)	**0.606***	-				
NR-WC (%)	**0.429†**	**0.765****	-			
Root precision (RII)	**0.759****	**0.561***	**0.481***	-		
Cladode ^{15}N (‰)	**0.603***	**0.408†**	0.176$^{n.s}$	0.378†	-	
Cladode N (%)	0.010$^{n.s}$	0.019$^{n.s}$	0.000$^{n.s}$	0.011$^{n.s}$	0.024$^{n.s}$	-
Cladode P (%)	0.014$^{n.s}$	0.050$^{n.s}$	0.112$^{n.s}$	0.001$^{n.s}$	0.036$^{n.s}$	**0.707****

* *P*<0.05; ** *P*<0.01; † - *P*<0.08 and **† *P*<0.065**

Thus, deuterium concentration in our experiment is indicative of the amount of water lifted to upper compartments. Two plants from the HL treatment had deuterium signatures that were similar to those in the NHL treatment (-13.35‰ and -24.65‰ respectively) indicating that they did not perform HL or had a limited ability to perform it, likely due to root damage when they were manipulated to create the air barrier between compartments. These plants also showed lower WC that was similar to those in the NHL.

These two plants were excluded from the ANOVA analyses but served us as a proxy for comparisons across treatments of the effects of HL on nutrient uptake and root growth processes.

At the end of the experiment, WC in discrete soil patches placed on the HL treatment was significantly greater than those in the NHL treatment, irrespective of OM addition (Fig. 1a, *Treatment* effect, *P*=0.038, Table 3 for ANOVA results). Nutrient-rich soil patches (NR) with OM-enriched in ^{15}N and P had significantly greater water content than soil-only patches without OM added (C patches, Fig. 1, *Patch effect P*<0.001). The interaction between the two factors was not significant (*Treatment x patch* effect, *P*=0.29), thus indicating that differences between treatments followed a similar trend in NR and C patches. Across treatments, *δD* in soils from the upper compartments was marginally correlated to WC in NR patches (Table 2, *P*=0.056).

Root growth into the NR and C soil patches and plant nutrient uptake

We detected a differential effect of treatments on root colonization of soil patches (Fig. 1b). Root colonization in soil patches was dependent on the presence or absence of OM (*Treatment x patch* effect, *P*<0.01, Table 4 for ANOVA results).

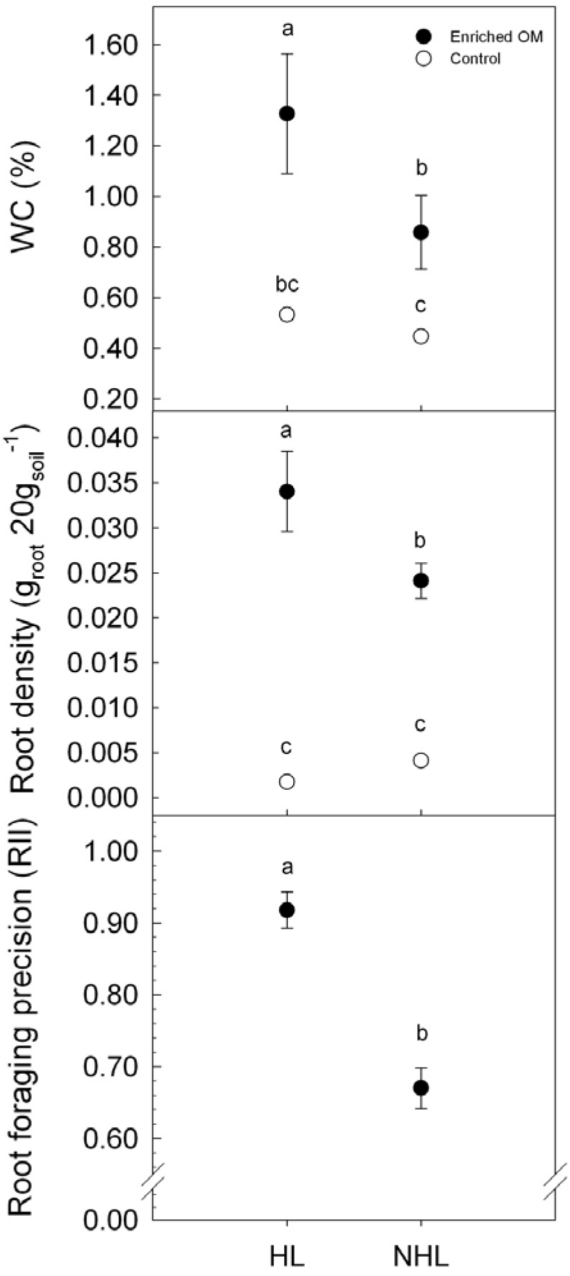

Fig. 1 Gravimetric soil water content (a), root density (b), and root foraging precision of *Retama sphaerocarpa* shrubs (c) in OM-enriched (closed circles) and control (open circles) soil patches in upper compartments. HL, Plants performing hydraulic lift; NHL, plants with impaired HL. Data are mean ± 1 SE (n=4 for NHL and n=3 for HL). Error bars are only shown when larger than symbol. Different letters indicate significant differences at *P*<0.05

Table 3. Factorial ANOVA results for gravimentric water content (%) in ^{15}N-enriched OM and control soil patches (*Patch*) collected in un-watered upper compartments in split-pots with *Retama sphaerocarpa* shrubs under two different treatments (HL, hydraulic lift and NHL, no hydraulic lift) (*Treatment*)

	df	MS	F	*P*-value
Model	3	0.754	11.348	**0.001**
Treatment	1	0.380	5.721	**0.038**
Patch	1	1.874	28.185	**<0.001**
Treatment x Patch	1	0.085	1.273	0.286
Error	10	0.066		

A significantly greater proportion of roots grew in NR patches of the HL treatment than of the NHL treatment (Fisher LSD post-hoc test, *P*=0.012). Moreover, OM in NR patches had a significant effect on root growth and a greater proportion of roots grew in NR than in C patches irrespective of the light treatment applied (*Patch* effect, *P*<0.001). Root foraging precision (RII) was significantly greater in shrubs that performed HL, which allocated 92% of the new root biomass grown in discrete soil patches into the nutrient-rich patches whereas shrubs in the NHL allocated approximately 67% (Fig. 1c). RII was positively correlated to δD and WC in soils from NR patches and from the upper compartments (Table 2).

Table 4. Factorial ANOVA results for root density (g_{roots} $20g_{soil}^{-1}$) in ^{15}N-enriched OM and control soil patches (*Patch*) placed in un-watered upper compartments in split-pots with *Retama sphaerocarpa* shrubs under two different treatments (HL, hydraulic lift and NHL, no hydraulic lift)

	df	MS	F	*P*-value
Model	3	0.00062	84.242	**<0.001**
Treatment	1	0.00004	5.293	**0.044**
Patch	1	0.00181	245.909	**<0.001**
Treatment * Patch	1	0.00009	11.988	**0.006**
Error	10	0.00001		

^{15}N content in cladodes before water and light treatments were applied was 4.58 ± 0.39 ‰, much lower than at the end of the experiment, when on average plants had 12.95 ± 2.17 and 7.10 ± 0.31 ‰ of ^{15}N in their cladodes in the HL and NHL treatments respectively (Table 5, $F_{1,8}$ = 24.69, *P*<0.001), suggesting a significant uptake of ^{15}N from NR patches. The amount of ^{15}N uptake by shrubs differed between treatments; after 10 weeks of drought, shrubs from the HL treatment had greater ^{15}N content than shrubs in the NHL treatment (Table 5).

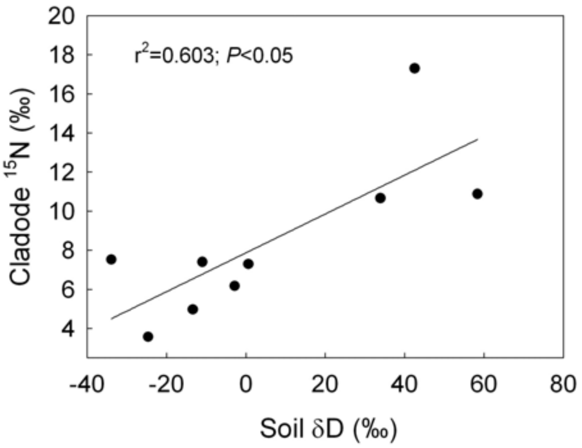

Fig. 2 Correlation between cladode ^{15}N content in *Retama* shrubs and soil water deuterium content (***δD***) in soils from un-watered upper compartments (n=9).

Across treatments, ^{15}N assimilation was strong and positively correlated to *δD,* and hence to the amount of water released in upper compartments via HL (Fig. 2), indicating a positive influence of hydraulically lifted water shed into the soil on ^{15}N uptake. ^{15}N uptake was marginally correlated to root foraging precision (Table 2, *P*=0.08). The amount of total N, P and C in cladodes followed a trend similar to that observed for ^{15}N; there was, however, there were no significant differences between treatments (Table 5, *P*>0.30).

Plant growth and physiological response

Plant water potentials (Ψ_p) remained relatively high (above -1 MPa) 10 weeks after water was withheld in the upper compartments, indicating that plants were not drought-stressed, although Ψ_p was significantly higher in shrubs growing under 12 h light than in shrubs growing under 22 h light (where hydraulic lift was partially suppressed; $F_{1,5}$=8.13, *P*=0.04). Photosynthetic efficiency of photosystem II (F_v/F_m) was around the optimum of 0.8 (Demmig & Björkman, 1987) in both treatments but significantly greater F_v/F_m was measured in shrubs in the HL treatment ($F_{1,5}$=6.75, *P*<0.05). No significant differences were detected in net photosynthetic rate (*A*) or stomatal conductance to water vapor (g_s) between treatments ($F_{1,5}$=0.14, *P*=0.73 and $F_{1,5}$=2.44, *P*=0.18 respectively; Table 6).

Total aboveground mass was not affected by treatments (Table 7, *P*=0.76). When divided into green (photosynthetic) and dry cladode mass, differences between treatments were not significant (*P*=0.86 and *P*=0.76 for green and dry biomass respectively). Total belowground mass, however, was greater in shrubs growing in the HL treatment than in the NHL (Table 7, *P*=0.03). Coarse (>2mm) and fine (<2mm) roots did not differ in upper compartments (*P*>0.30 in both cases) but fine roots significantly differed in the lower compartments (*P*<0.01) but not coarse roots (*P*=0.69). Differences in fine root biomass did not affect the root-to-shoot ratio (R:S) which did not differ between treatments (*P*=0.74).

Discussion

Our results show that *Retama sphaerocarpa* shrubs performed hydraulic lift and that continuous illumination successfully suppressed, or to some extent reduced, this process. Root foraging precision was greater in shrubs performing HL, which showed greater root colonization of nutrient-rich patches than shrubs with reduced HL ability. ^{15}N assimilation was also enhanced in shrubs that performed HL, which took up twice as much ^{15}N as those that did not perform HL.

Table 5. ^{15}N content (‰) in cladodes and roots and total nitrogen (N), carbon (C) and phosphorus (P) content (%) in mature *Retama sphaerocarpa* cladodes collected one week before treatment application (t_0) and at the end of the experiment in shrubs performing hydraulic lift (HL) and with impaired HL (NHL). Total N content (%) in roots is also shown. Data are mean ± 1SE (n=4 except for HL where n=3). Different letters in a row show significant differences between treatments (one-way ANOVA, *P*<0.05)

	t_0	*HL*	*NHL*
Cladode ^{15}N (‰)	4.58 ± 0.44^a	12.95 ± 2.17^b	7.10 ± 0.31^c
Cladode N (%)	2.24 ± 0.15^a	2.62 ± 0.18^a	2.48 ± 0.10^a
Cladode P (%)	0.08 ± 0.01^a	0.09 ± 0.01^a	0.09 ± 0.01^a
Cladode C (%)	44.82 ± 0.21^a	45.85 ± 0.40^a	45.62 ± 0.95^a
Root ^{15}N (‰)	n.a	22.17 ± 3.63^a	19.17 ± 2.89^a
Root N (%)	n.a	1.67 ± 0.08^a	1.65 ± 0.03^a

n.a – not available

Table 6. Plant water potential (Ψ_p), photosynthetic efficiency of photosystem II (F_v/F_m), net photosynthetic rate (A) and stomatal conductance to water vapor (g_s) measured in green mature cladodes from *Retama sphaerocarpa* shrubs growing under 12h of light (HL) and 22h of light (NHL). Data are mean ± 1SE (n=3 for HL and n=4 for NHL). Different letters in a row indicate significant differences between treatments for each variable (one-way ANOVA, *P*<0.05).

	Treatment	
	HL	**NHL**
Ψ_p	0.48 ± 0.05^a	0.76 ± 0.07^b
F_v/F_m	0.84 ± 0.00^a	0.82 ± 0.01^b
A	2.71 ± 0.28^a	2.37 ± 0.74^a
g_s	0.03 ± 0.01^a	0.05 ± 0.01^a

A strong linear relationship between magnitude of HL (measured as δD concentration) and soil water content, root foraging precision (RII) and ^{15}N uptake indicated that only plants that performed HL used the extra source of water in the upper compartments, which played a significant role in promoting root growth into - and nutrient uptake from- NR patches. Greater water availability in the upper compartments, and arguably greater nutrient OM mineralization in NR patches in HL-performing shrubs led to greater root growth in soil patches where nutrients were readily available, and thus to greater ^{15}N uptake.

Deuterium is not dicriminated when water is taken up and released through HL, and thus, it can be used as an effective tracer to determine plant water sources (Dawson *et al.*, 2002). The application of heavy water in deep soil layers and its detection in upper soil layers when the only pathway for water movement is through plant

Table 7. Above- and belowground plant mass, green and senesced cladode mass, and fine (<2 mm) and coarse (>2 mm) root mass from upper and lower pot compartments of *Retama sphaerocarpa* shrubs performing hydraulic lift (HL) and with HL impaired (NHL). Data are mean ±1 SE (n=4 for NHL and n=3 for HL). Different letters in a row show significant differences between treatments (one-way ANOVA, $P<0.05$)

	Treatment	
mass (g)	***HL***	***NHL***
Total aboveground	9.32 ± 1.29^a	10.24 ± 2.03^a
Green	7.24 ± 1.43^a	7.19 ± 1.92^a
Dry	3.01 ± 0.89^a	2.13 ± 0.72^a
Total belowground	19.94 ± 1.84^a	13.87 ± 1.27^b
Upper compartments		
Fine roots (<2mm)	3.13 ± 0.68^a	1.99 ± 0.40^a
Coarse roots (>2mm)	6.05 ± 0.44^a	5.07 ± 0.29^a
Lower compartments		
Fine roots (<2mm)	8.61 ± 1.40^a	4.70 ± 1.20^b
Coarse roots (>2mm)	2.04 ± 0.46^a	1.81 ± 0.34^a
R:S ratio (Green)	3.42 ± 0.92^a	3.16 ± 1.43^a

roots has been used to evidence HL (Dawson, 1993, Filella & Peñuelas, 2003, Leffler *et al.*, 2005).

In our study, after application of enriched water to the lower compartments (≈ 5000 ‰), greater positive *δD* values were found in the upper compartments of pots where HL was allowed, providing evidence of HL in shrubs growing under 12 h of light (HL treatment). We did not measure background *δD* levels but differences between treatments provide clear evidence that greater amounts of water were released when HL was not inhibited by continuous illumination. In addition, WC was also significantly greater in the HL treatment, both in upper compartments and in discrete soil patches, even after a relatively long drought period. When comparing soil moisture in the HL treatment with its control without shrubs (S12), the latter were significantly drier and significantly lower WC values were observed in the NHL treatment, similar to its control without shrub (S22).

Isotopic data show that soil in the HL treatment was wetted by water lifted by the plant from the permanently wet lower compartments. The tight relationship between *δD* and WC in upper compartments across treatments supports this idea, and it is a clear indication that only plants performing HL were able to maintain higher soil moisture in upper compartments, and that water transported through HL from lower compartments was the source of this extra soil moisture. We can then conclude that *Retama* shrubs performed HL under 12 h of light (HL treatment) whereas continuous illumination at night (NHL treatment) stopped the process and that these differences led to greater soil water availability in upper compartments of the HL treatment.

Plants actively forage for resources in heterogeneous environments (Hodge, 2010, Robinson, 1994, Bauerle *et al.*, 2008b, Hutchings *et al.*, 1994) and roots proliferate in resource-rich soil patches at the expenses of root growth in resource-poor patches (Drew, 1975). In our study, *Retama* shrubs displayed an active foraging behavior observed by the positive root foraging precision (RII) and greater root colonization into NR patches compared to soil-only C patches. The root foraging precision of shrubs was enhanced in individuals that lifted water more than in individuals that did not, where root foraging precision was 25% lower, thus confirming our first hypothesis. When analyzed across treatments there was a tight correlation between δD in soil water and root foraging precision (RII) suggesting that greater availability of water through HL promoted root colonization into NR soil patches. Therefore, hydraulically lifted water enhanced the ability of *Retama* to grow roots into these nutrient-rich soil patches.

There was, however, also root growth in NR patches in the NHL treatment, suggesting that HL was not the only mechanism affecting root foraging behavior in NR patches. The most likely explanation is related to OM decomposition processes in nutrient rich soil patches. In a similar study with buffalo grass (*Buchloe dactyloides*), nitrogen mineralization in plants performing HL was highly dependent on soil moisture conditions (Armas *et al.* unpublished). In our case, greater HL maintained greater soil moisture in NR patches which could have enhanced OM decomposition and mineralization (Aanderud & Richards 2009) leading to greater N availability. Not surprisingly, we observed a positive correlation between the amount of water shed into upper soil layers through HL (measured as δD), plant ^{15}N assimilation and root foraging precision. Besides, although shrubs from both treatments assimilated significant amounts of ^{15}N during the several weeks of the study, plants that performed HL assimilated twice as much than plants that did not, evidencing that HL enhanced nutrient availability from NR patches. These data suggest greater nutrient availability for the shrubs in NR patches is a consequence of greater HL that triggered greater root foraging precision in such shrubs.

In summary, we have provided direct evidence that *Retama sphaerocarpa* actively forages for nutrients and that, under drought conditions, water provided through HL helps root proliferation in nutrient-rich patches in heterogeneous soils. To our knowledge, this is the first direct evidence linking the ability of plants to perform HL with root growth and foraging processes. This mechanism can be important to species with access to deep-water sources and able to perform HL that might benefit from the selective placement of roots in nutrient-rich patches and increased nutrient uptake even during drought periods when root growth and nutrient uptake are usually limited. In Mediterranean ecosystems with longer drought periods in between rain events and a prolonged summer drought, this capacity might confer a competitive ability and greater survival rates to species performing HL. Opposite, species with no access to deep-water reserves or lacking the ability to perform HL may be competitively displaced.

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Adult *Retama sphaerocarpa* shrub (aprox. 2 m tall) growing in a field site near Almeria, Spain (left) and a three-year old shrub growing in a experimental split-pot in the greenhouse (right)

Capitulo IV

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*Contribución de el levantamiento hidráulico en la facilitación por una especie nodriza en un ambiente semi-árido**

*Enviado como: Prieto I, Padilla FM, Armas C, Pugnaire FI (2010) Contribution of hydraulic lift to facilitation by nurse plants in a semi-arid environment

Capítulo IV

CONTRIBUTION OF HYDRAULIC LIFT TO FACILITATION BY NURSE PLANTS IN A SEMI-ARID ENVIRONMENT

Summary

Hydraulic lift (HL) has been shown to improve performance of individuals occurring next to a lifting plant, but whether this process plays a role in seedling establishment and growth remains unknown. Here, we tested the influence of HL on the interaction between *Retama sphaerocarpa*, a nurse lifter shrub from semi-arid Spain, and the evergreen shrub *Marrubium vulgare.* Seedlings of *Marrubium* were planted under the canopy of *Retama* in three tube types that reduced or fully prevented competition and that allowed or prevented the flux of water from entering the tube. Additional seedlings in gaps between shrubs served to evaluate the overall facilitative effect of the nurse shrub. HL patterns were observed under the canopy of *Retama* only in tubes that allowed the flux of hydraulically lifted water. Seedling survival was greatest in the treatment where competition was reduced and HL allowed or where these were fully prevented. Seedling biomass was greatest in the treatment where seedling grew isolated from nurse's roots, with no competition and no HL, followed by the treatment where competition was reduced and HL allowed. Seedling mass was lowest in the treatment where full interactions were allowed. These results show intense competition for water between *Marrubium* seedlings and neighbouring roots, and also a significant contribution of HL to seedling survival but not to seedling mass. Overall, the extra water supplied via HL did not fully counterbalance competition by neighbours. However, despite competition, *Marrubium* seedlings performed better under the canopy of *Retama*, where microclimate conditions were ameliorated and soil water content was higher than in gaps. Overall, this facilitation mechanism reduced the intense competition for water under the canopy of *Retama* and had important implications for plant community structure and composition

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Introduction

Hydraulic lift (HL) is a process by which plants take up water from deep, moist soil layers and passively transport and release it into shallow, drier soil layers (Richards and Caldwell 1987). HL could be beneficial for both the lifting plant and its neighbours (Caldwell et al. 1998, Ryel 2004) although reports on whether the net effect for neighbours is positive are not fully conclusive (Dawson 1993, Ludwig et al. 2004, Zou et al. 2005, Schoonmaker et al. 2007). For plants lifting water, HL can increase transpiration by providing an additional water source in the upper soil (Caldwell and Richards 1989, Ryel et al. 2002) as well as temporary water storage during drought periods (Brooks , Meinzer & Coulombe 2002, Meinzer et al. 2004). This additional water is effective in maintaining fine root function (Caldwell et al. 1998, Bauerle et al. 2008) and reducing xylem embolism in shallow roots (Domec, Warren & Meinzer. 2004) as well as allowing survival of root symbionts (e.g., mycorrhizal fungi) in otherwise dry soil (Querejeta, Egerton-Warburton & Allen 2003, Querejeta, Egerton-Warburton & Allen 2007).

Hydraulically lifted water can also be used as an additional supply by the lifter's neighbours (Caldwell 1990, Dawson 1993) as documented both in greenhouse (Hirota et al. 2004, Egerton-Warburton, Querejeta & Allen 2007) and field studies (Caldwell 1990, Warren et al. 2008, Hawkins et al. 2009). But HL not only has positive effects on neighbours (Dawson 1993, Zou et al. 2005); they could be neutral (Schoonmaker et al. 2007, Fernández et al. 2008) or even negative (Ludwig et al. 2003, Ludwig et al. 2004, Armas et al. 2010) suggesting that the net balance of the interaction among lifter species and its neighbours may be species-specific and context dependent. These diverse outcomes of HL highlight the need for further studies on its effects, a topic that may be of paramount importancefor better understanding plant interactions in water-limited ecosystems where, along with shallow-rooted species many deep-rooted species co-exist that can tap groundwater (Haase et al. 1996, Jackson et al. 1999) and potentially perform HL (Hultine et al. 2004, Prieto, Kikvidze & Pugnaire 2010a).

Hydraulic lift has been suggested as a facilitation mechanism that allows preferential seedling recruitment under the canopy of lifter plants acting as nurses (Dawson 1993, Caldwell et al. 1998, Callaway 2007) but the effects of HL on seedling establishment have not been directly tested yet, nor has been quantified the extent to which HL contributes to the facilitation effect of nurse plants (Ryel 2004, Callaway 2007). Plant interactions are complex and commonly comprise reciprocal positive and negative effects between the interacting species (Aguiar, Soriano & Sala1992, Armas and Pugnaire 2009, Armas et al. 2010), being the outcome of the interaction (e.g., facilitation, competition) the net balance of all positive and negative effects (Holmgren, Scheffer & Houston1997, Holzapfel and Mahall 1999, Pugnaire and Luque 2001). We could expect that the balance between positive and negative effects of HL to be of especial relevance in arid systems where water availability is a main factor regulating seedling establishment (Moles and Westoby 2004, Padilla and Pugnaire 2007).

We addressed whether HL had a net positive effect in the interaction between a nurse plant species and seedlings in its understory. We used a well-known system consisting of the large nurse shrub, *Retama sphaerocarpa* L. (Boiss), and the understory protégée shrub, *Marrubium vulgare* L. (Pugnaire, Haase & Puigdefábregas 1996a). *Retama* facilitates the establishment and growth of many shrub and herbaceous species (Pugnaire et al. 1996a, 1996b, Pugnaire and Lázaro 2000, Rodriguez-Echeverria & Pérez-Fernández 2003). Amelioration of microclimatic conditions and increased resource availability under *Retama* canopies accounted for facilitative interactions (Moro et al. 1997a, 1997b, Pugnaire, Armas & Valladares 2004), although the role of hydraulic lift by *Retama* (Prieto et al. 2010a) in the facilitation process remains unaddressed.

Here we tested whether HL had a net positive effect on survival and growth of *Marrubium* seedlings occurring under the nurse shrub by conducting a field experiment in which we creatively manipulated the interaction between understory seedlings and overstory *Retama* shrubs. By using tubes with different mesh size we altered belowground interactions by preventing or reducing competition at the same time that we prevented or allowed hydraulic lift or by allowing both competition and HL. We hypothesized that HL would have a positive effect on *Marrubium* survival and growth under the canopy of *Retama.* We expected i) greatest survival and growth when belowground competition was fully prevented, even in the presence of hydraulically-lifted water; ii) greater seedling survival and growth when hydraulic lift was allowed and belowground competition was reduced as seedling would take full advantage of hydraulically lifted water with reduced competition iii) lower survival and growth rates under full belowground competition conditions as seedlings would take full advantage of hydraulically lifted water but competition for water would be greatest; and iv) the lowest survival and growth would be found in seedlings growing in gaps where microclimate conditions are expected to be harsh and seedlings would not benefit from hydraulically-lifted water

Materials and methods

Study site and species

The field site was located in Rambla del Saltador, Almeria province, SE Spain (lat 37º 08'N, long 2º 22' W, 630 m altitude). The site is a dry valley located south of the Filabres Range over micaschist bedrock where slope erosion produced big alluvial fans and colluvial deposits. The soil in the bottom of the valley is from alluvial origin and of a loamy sand texture (Puigdefábregas et al. 1996). The climate is semi-arid with a mean annual precipitation of 245 mm comprising a dry period in summer, from June to August (Haase et al. 1999). Mean annual temperature is 18.2 ºC (Pugnaire & Lázaro 2000).

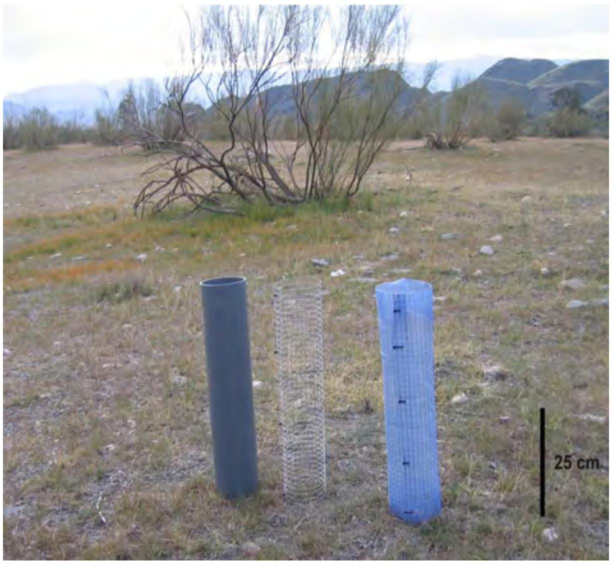

Fig 1. Picture of the field site with *Retama phaerocarpa* shrubs in the background and the three different types of tubes used in this experiment (forefront). Left, PVC tube that did not allow root trespassing or water flow; center, Mesh tube that allowed neighbouring roots to get inside the tube and free movement of water; right, Net tube that did not allow root trespassing into the tube but allowed free transfer of water between soil inside and outside the tube. Note the clear facilitative effect of *Retama* shrubs on the understory plant community compared to gaps between the nurse shrubs

The community in the riverbed and alluvial terraces is dominated by the legume *Retama sphaerocarpa* (L.) Boiss (Figure 1), a large shrub occurring in the Iberian Peninsula and northwest Africa. It has an open canopy with photosynthetic stems and a dimorphic root system composed by shallow lateral roots and tap roots that can well reach 30 m depth (Haase et al. 1996). Roots of this species are able to lift water from wet layers and release it into dry soils (Prieto et al. 2010a, 2010b). The areas between shrubs are barely vegetated and most of the woody and herbaceous species are below the canopy of *Retama*. This species has been shown to facilitate the growth and survival of plants under its canopy (Pugnaire et al. 1996b, Padilla and Pugnaire 2009). One such species facilitated by *Retama* is our target species, *Marrubium vulgare* L., a woody perennial plant up to 1 m high (Pugnaire et al. 1996a).

Experimental design

Three different types of tubes were used in soils under *Retama*´s canopy (Figure 1). One tube consisted of a cylindrical metal mesh, 10 mm mesh size, covered with a thin cloth 200µm mesh size that did not allow root trespassing into the tube but allowed free transfer of water between soil inside and outside the tube. This treatment (Net, hereafter) prevented root competition and allowed any influence of HL on seedlings. The second type of tube consisted of the same cylindrical metal mesh but without cloth. This treatment (Mesh, hereafter) allowed neighbouring roots to get inside the tube and free movement of water. This treatment allowed for full competition between target seedlings and neighbours while at the same time allowed the HL effect. The third treatment consisted of a PVC cylindrical tube that did not allow root trespassing or water flow. In this treatment (PVC, hereafter), neither HL nor competition with neighbouring roots occurred due to the physical barrier. These three tube types were all 50 cm long and 12.5 cm internal diameter and open in their bottom to allow free drainage of water vertically in the soil profile.

A total of 34 *Retama* shrubs were randomly selected in a 1-ha homogeneous, flat alluvial terrace within the Rambla del Saltador field site. Beneath each shrub, three 60 cm deep x 20 cm diameter holes were drilled with an automatic auger (Stihl, BT121, Andreas Stihl Ag & Co. Waiblingen, Germany) in three different azhimutal directions (N, E, W) in February 2008. Additionally, holes were excavated in open spaces between shrubs (Gaps, hereafter) at least 6 m away from the closest *Retama* individual, far away from the influence of facilitative and competitive effects from the nurse shrub. Holes under *Retama* shrubs were made within a 50 cm distance from the base of the shrub’s main trunk. One type of each experimental tube was then randomly assigned and inserted into each hole, refilled with original soil, and compacted to original bulk density. Each shrub had therefore the three treatments under its canopy. In gaps, only Mesh tubes were inserted following the same procedure. The site was allowed to stabilize for 8 months before plantation in autumn 2008.

In September 2008, seeds of *Marrubium vulgare* were germinated on vermiculite (Verlite®, Vermiculita y Derivados SL, Gijón, Spain) in the greenhouse. One month after emergence, height (mm) and biomass (g) were measured in 10 randomly selected seedlings. Seedlings were then taken to the field and three seedlings were planted inside each tube. Sixty ml of water were then supplied to each tube to help seedling establishment. Upon plantation, seedlings were protected against herbivores with a mesh cage 18 cm width x 15 cm high, 2 cm mesh size. Fifteen days after planting, dead seedlings were replaced to ensure seedling establishment. In late October, once overcome transplant shock, seedlings were thinned to one per treatment. Cages were kept throughout the experiment and no water was ever supplied other than the 60 ml supplied to help seedling establishment.

Soil moisture and micrometeorology

Soil water potential (Ψ_s) was measured at regular intervals on the course of the experiment using thermocouple psychrometers (PST-55 (-SF); Wescor, Logan, UT, USA) installed at 40 cm depth inside the tubes under four *Retama* shrubs. Psychrometers were inserted at this depth because roots of *Marrubium* are able to reach such depth soon after plantation (*pers. obs.*) and patterns of hydraulic lift in *Retama* are strongest at such depth and were not detected below 80cm (Prieto et al. 2010b).

Each psychrometer was individually calibrated in the laboratory against salty solutions of known molality following Brown & Bartos (1982). Psychrometers were installed in the field on February 2008 and left to stabilize for 8 months until beginning of the experiment. Psychrometers were then connected to a data logger (CR7, Campbell Scientific Inc, Logan, UT, USA) and soil water potential was recorded at hourly intervals for a period of 2 to 3 consecutive days twice during winter and every month during spring and summer. Additionally, at harvest, gravimetric soil water content (%) was determined in sixteen soil samples obtained from four tubes of each treatment underneath *Retama* and four tubes in gaps between shrubs. Soil was collected with a corer sampler (AMS Inc, American Falls, ID, USA) at 10 cm depth and weighed immediately after collection. Samples were taken to the lab and oven-dried at 105ºC for 72 h and weighed again. Gravimetric water content (%) was obtained as the weight difference (g) between wet and dry soil per unit dry soil (g).

Air temperature and relative humidity were recorded (Onset Computers Co., Pocasset, MA, USA) during winter and summer for two to three consecutive days every 30 minutes under the canopy of shrubs and in gaps (n = 3). Photosynthetically active radiation was recorded in the same microsites with appropriate sensors (SKP 215 PAR Quantum, Skye Instruments Ltd. Powys, UK). Measurements were taken every 30 seconds and a mean value was recorded every 10 minutes (AM16/32 and CR10X data logger, Campbell Scientific Inc, Logan, UT, USA).

Seedling survival, growth and physiological measurements

Living and dead seedlings were recorded every 15 days beginning in November 2008 and encompassing autumn establishment, spring growth and summer drought. Seedlings that died between two consecutive sampling dates were collected, oven dried at 70ºC for 72 hours and weighed to determine dry mass (g). Height (mm) of living seedlings was measured from the soil surface to the base of the most distal part of the stem bimonthly during autumn and spring and on a monthly basis during summer. The following allometric relationship was obtained between height (mm) of living seedlings and biomass (g) of recently dead seedlings: *Biomass* = 0.0065 x *Height* (R^2=0.64, $p<0.01$). Here we assume that no significant mass loss happened in dead seedlings between sampling dates. This equation was used to estimate seedling biomass of living seedlings at each sampling date.

Statistical analysis

Differences in *Marrubium* seedling survival among the different treatments over time were analyzed using the Kaplan-Meier analysis function with "*treatment*" as the factor and "*day from seedling establishment*" (e.g., end of the transplant shock period, October 2008) as the time effect. Previously, a Kaplan-Meier analysis did not detect any effect of aspect on survival, and thus this factor was not included into analyses. The Kaplan-Meier analysis was followed by pairwise comparisons between treatments using the Log-Rank test function. Significance of pairwise comparisons were then corrected by Bonferroni after adjusted by Legendre & Legendre (1998).

At harvest, differences in seedling survival among treatments were tested using binary logistic regression, where treatment was the categorical factor and survival was the response variable, followed by pairwise comparisons between treatments and the aforementioned correction. Seedling growth over the study period was analyzed using ANCOVA analyses, with "*treatment*" as the factor and "*sample date*" (day from seedling establishment) as the covariate. Differences in seedling growth over the experiment were considered significant when the "*treatment x date*" interaction was significant (Garcia-Serrano 2005). Differences in soil water potential among different treatment tubes over the experiment was analyzed using repeated-measures ANOVA with "*time*" as between effects. PAR radiation, temperature (ºC) and relative humidity (RH) were analyzed using a Student's t-test (under *Retama* canopy *vs.* in gaps) on each sampling date, as repeated-measures ANOVA could not be performed due to low replication. Gravimetric water content (GWC) was analyzed using a Student's t-test.

Data were analyzed with SPSS v.17.0 (SPSS Inc., Chicago, IL, USA). Results are presented as mean values ± 1 SE throughout.

Results

Hydraulic lift and soil moisture

Hydraulic lift was detected in the Net and Mesh treatments from April to June but not in the PVC treatment nor in any treatment in winter months (Figure 2). In the two former treatments, soil water potential decreased during daytime and increased at night, a pattern classically attributed to hydraulic lift. On the other hand, in the PVC treatment soil water potential decreased day and night. These data evidence that *Retama* roots were responsible for hydraulic lift, as it did not happen in the treatment where roots of *Retama* were excluded (PVC tubes).

The summer period was very dry and most psychrometers remained inoperative presumably because soil water potential dropped below -6 MPa, a value close to the lower limit for

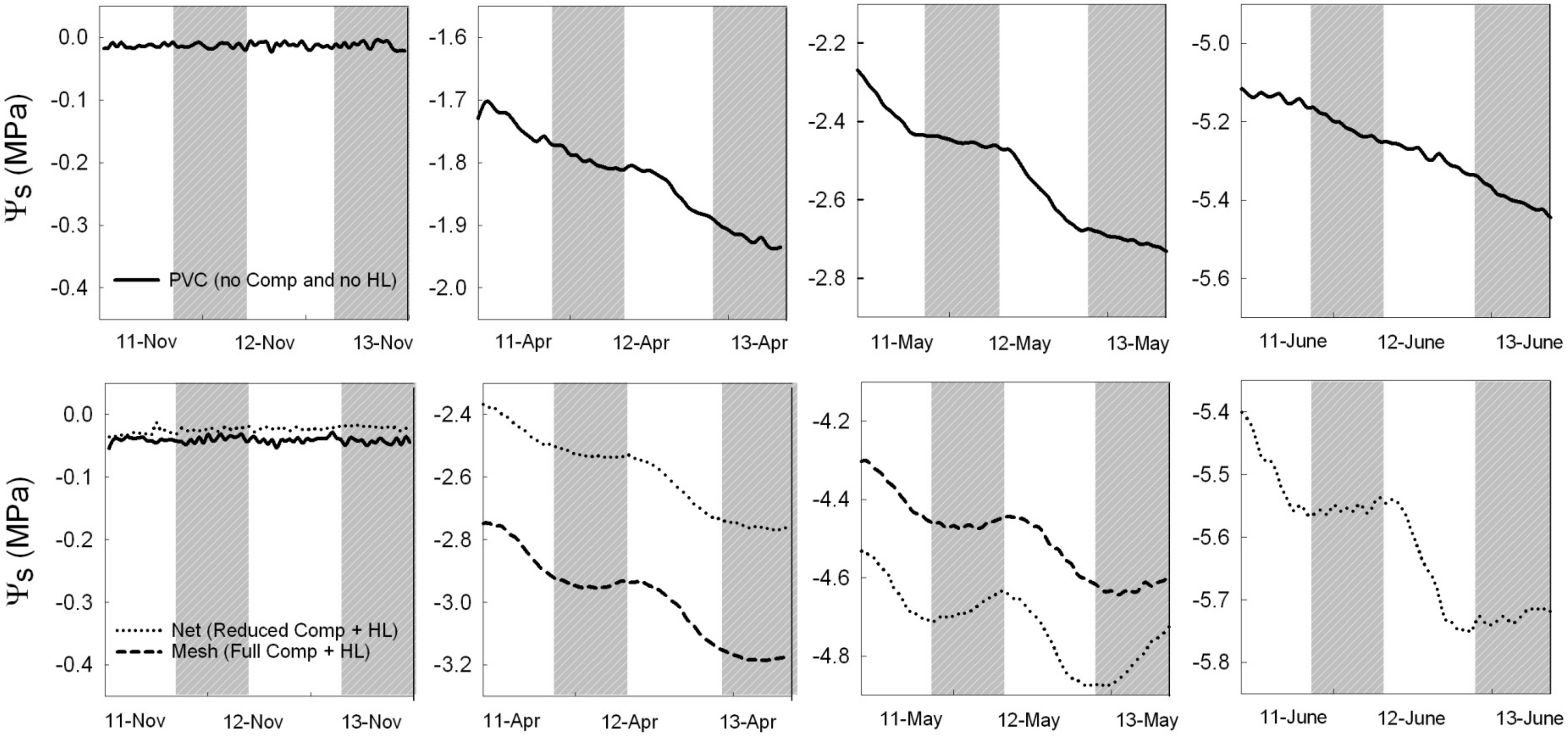

Figure 2. Mean soil water potential (n=4 except for Mesh in May, where n=3, and June,where n=1) measured at hourly intervals at 40cm depth inside treatment tubes. Hydraulic lift (HL) cycles (e.g., increased soil water potential at night) were only detected in Mesh and Net tubes (lower panels). Dark areas indicate nighttime. Note the different scales in the y-axis. Representative SE are shown in Table 1

psychrometric measurements (Brown and Bartos, 1982). Hydraulic lift was not observed in winter most likely because shallow soil layers were completely moist (Table 1).

Soil water potential under *Retama* was significantly different among treatments ($F_{2,\ 8}$ = 4.77, $P < 0.05$) and changed on the course of the experiment ($F_{2,\ 16}$ = 144.32, P<0.001). In addition, the pattern of soil drying differed among treatments, as indicated by the significant "*treatment x date*" interaction ($F_{4,\ 16}$ = 4.85, P<0.01, Table 1). Overall, soils remained moist (above -0.05 MPa) during winter in all treatments and got dryer as seasonal drought progressed. Soil in the PVC treatment was moister than in Net and Mesh treatments, without significant differences between these two latter on the sampled dates (Table 1). Gravimetric water content measured at harvest time was significantly higher under the canopy than in gaps (Table 2).

On average, year 2009 was wet with a total of 293 mm of rain, well above the 245 mm average described for the study site (Lázaro et al. 2001); 287 mm fell during winter and spring and only 6 mm from May to mid-September (Figure 3), Microclimatic conditions were less severe under shrub canopies than in gaps. The canopy of *Retama* reduced some of the photosynthetically active radiation (PAR), which was 35% and 42% lower under the canopy than in gaps in winter and summer, respectively (Table 2). Mean day temperatures were lower under the shrubs and mean relative humidity was significantly higher under the canopy than in gaps. Differences in both variables were significant during summer but not in winter. Daily changes in temperature, measured as the difference between the daily maximum and minimum, were 5ºC greater in gaps than under the shrub canopy in summer. No significant differences were observed in winter.

Microclimatic conditions

Table 1. Mean daily soil water potential ± 1SE (Ψ_s, MPa) measured at 40 cm depth in treatment tubes under *Retama* shrubs from November 2008 until June 2009. Different letters indicate significant differences between treatments within each date, and a cross next to the letter indicate marginally significant differences within each date (RM-ANOVA, M-ANOVA Tukey post-hoc test, 0.05<P<0.1 for marginally significant differences; n=4 except in May where n=3). Data from June 2009 was not included in the analysis due to the low number of replicates.

	Ψ_s (MPa)			
Treatment	**Nov**	**Apr**	**May**	**Jun**
PVC (No comp and no HL)	-0.01 ± 0.01a	-1.82 ± 0.40a	-2.54 ± 0.66a	-5.27
Net (Reduced comp + HL)	-0.04 ± 0.06a	-2.59 ± 0.34a	-4.72 ± 0.07b+	-5.61
Mesh (Full comp + HL)	-0.02 ± 0.03a	-2.99 ± 0.26a	-4.13 ± 0.41b+	–

Table 2. Microclimate conditions measured under *Retama* shrubs and in gaps in winter and summer. Variables are: maximum photosinthetically active radiation (PAR), mean day temperature (T), mean relative humidity (RH), daily temperature difference (Daily T diff) and gravimetric soil water content (GWC). Data are mean ± 1SE (n=3). Data for GWC under shrubs were obtained by pooling data from the three treatment tubes (n=4). Different letters denote significant differences for each variable between microsites within each season (t-test, $P<0.05$)

	Winter		**Summer**	
	Retama	**Gaps**	***Retama***	**Gaps**
PAR (µmol m^{-2} s^{-1})	985.50 ± 159.13a	1523.95 ± 13.85a	1048.11 ± 61.14a	1795.88 ± 94.85b
T (ºC)	20.50 ± 0.16a	21.40 ± 0.48a	35.00 ± 0.32a	38.65 ± 0.40b
RH (%)	65.63 ± 7.54a	64.19 ± 2.54a	11.72 ± 0.39a	9.10 ± 0.50b
Daily T diff (%)	11.86 ± 0.30a	11.49 ± 1.23a	20.52 ± 0.68a	26.05 ± 1.10b
GWC (%)	-	-	0.33 ± 0.03a	0.16 ± 0.02b

Seedling survival and growth

There were significant differences in seedling survival among treatments on the course of the experiment (Kaplan-Meier, $\chi^2=21.98$, $P<0.001$; Figure 3). In winter and spring around 60-80% of the seedlings were alive whereas at the beginning of the dry season seedling mortality increased, especially in the treatments where full competition took place (Mesh tubes) or where abiotic conditions were harsher (Gaps); in these treatments survival by late June was reduced to 37% and 7%, respectively, whereas survival in PVC and Net tubes was 57% and 63% respectively. Survival differences were greatest among treatments at the end of the summer, after more than 4 months of drought (logistic regression, $\chi^2=6.31$, $P<0.01$). Overall, *Marrubium* seedlings had greatest survival rates in PVC and Net tubes with 33% and 30% of seedlings surviving the summer drought, and lowest survival rates in Mesh tubes and in gaps. In other words, survival was highest when belowground competition was either prevented or reduced by solid-walled PVC tubes or by Net tubes, this latter allowing the transfer of hydraulically lifter water. It is worth noting that in gaps no seedling survived at the end of the experiment while final survival in Mesh tubes reached 7%.

Seedling growth in winter was slow but a great increase in biomass did occur in spring. Biomass increased five-fold in the PVC treatment vs. three-fold in the Net treatment and less than two-fold in Mesh tubes and in gaps. During summer drought, seedling growth remained almost steady in all treatments. An increase in seedling biomass was observed in the Mesh treatment towards the end of the experiment, but this fact may likely be due to a differential mortality of smaller seedlings in this treatment rather than to a true gain of mass (data not shown). Seedling growth changed with time in the different experimental treatments as indicated by the significant interaction "*treatment x day*" (ANCOVA $F_{3, 613}=4.207$, $P<0.01$, Figure 2).

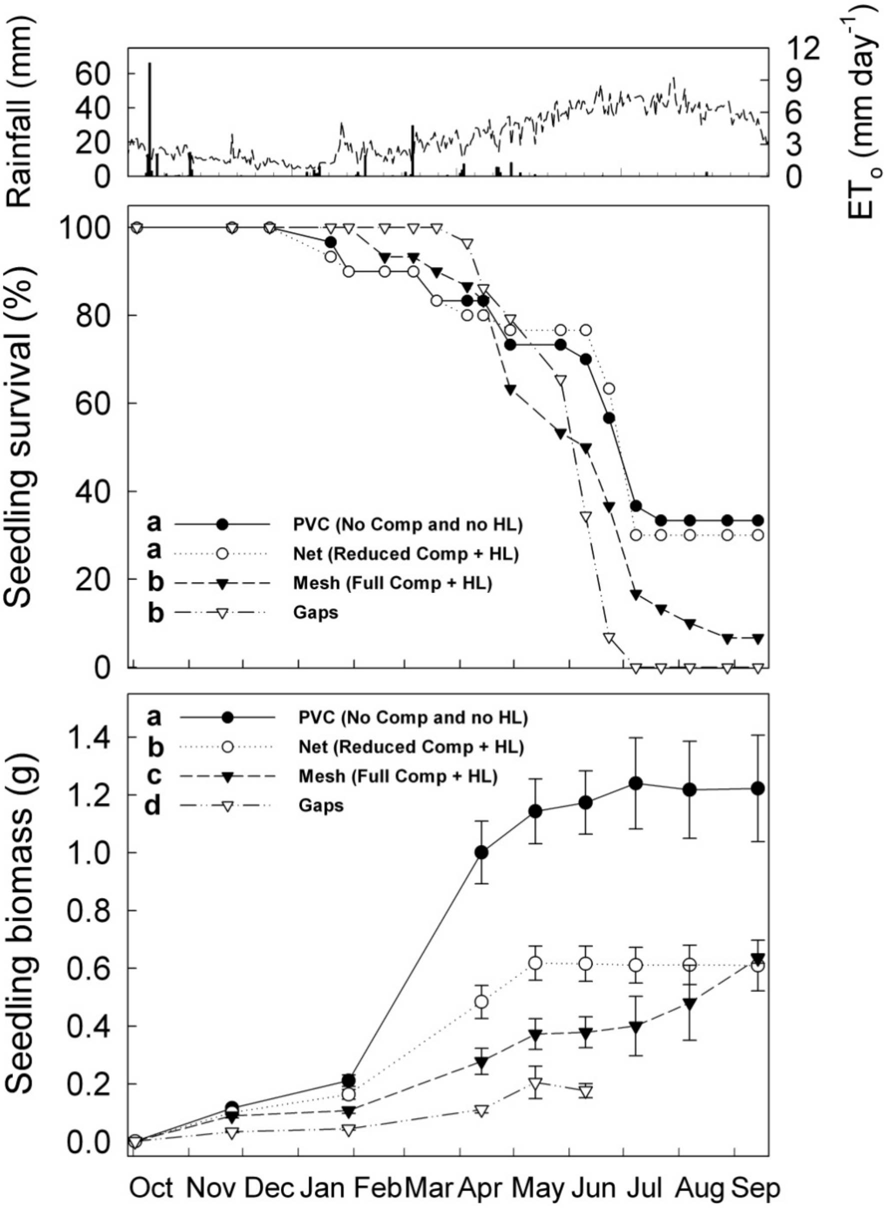

Fig 3. Rainfall (dark bars, upper panel) and evapotranspiration (dashed line, upper panel), seedling survival (middle panel) and biomass (lower panel) of surviving *Marrubium vulgare* seedlings planted in three different tube treatments under *Retama sphaerocarpa* shrubs (PVC, Net and Mesh) and in Gaps. Data for biomass are mean ± 1SE. Different letters indicate significant differences among treatments (log-rank test for survival, $P<0.001$; Scheffé post-hoc test for seedling biomass, $P<0.001$). Rainfall and evapotranspiration data were collected from an adjacent meteorological station, IFAPA.

Seedlings growing where hydraulic lift and decreased competition took place (Net tubes) gained significantly more biomass than seedlings growing in tubes where full competition occurred (Mesh tubes) or in gaps. On the contrary, seedlings growing with no effect of hydraulic lift but no belowground competition (PVC tubes) grew the most, significantly more than seedlings in Net tubes.

Discussion

We found that *Retama sphaerocarpa* shrubs enhanced both survival and growth of *Marrubium vulgare* seedlings in its understory compared to seedlings growing in gaps. All seedlings that survived summer drought were in the understory of *Retama,* whereas no one survived in gaps. Therefore, consistently with previous results, *Retama* acted as a nurse facilitating the establishment and growth of *Marrubium* seedlings in its understory. This facilitation effect was likely caused by ameliorated microclimatic conditions and greater moisture availability (Pugnaire et al. 1996a, Moro et al. 1997a). The greater soil moisture under *Retama* was due to shade that lowered evaporation –e.g., soils in tubes with no HL (PVC) had greater WC than gaps– but mainly by HL (e.g., in Net and Mesh treatments; Table 2 and Figure 2). Other mechanisms, however, may have also influenced survival under *Retama*, such as greater nutrient availability and improved soil physical and chemical conditions (Pugnaire et al. 1996b, Moro et al. 1997a, 1997b, Pugnaire et al. 2004).

Total exclusion of *Retama* roots in PVC tubes prevented belowground competition from the nurse shrub so that depletion of soil moisture inside these tubes was lower than in treatments where competition for water occurred (Mesh and Net) despite HL also took place. This led to greater soil water potentials inside these tubes (PVC) in spring and summer and greater seedling growth, albeit seedling survival was similar in PVC and Net tubes despite the latter having lower soil water potentials. In treatments where HL was present (Net and Mesh), soil moisture remained higher, and survival and growth was greater than in gaps at the end of the summer. Hydraulic lift under the canopy of *Retama* thus buffered soil moisture depletion by replacing at night –when HL occurs- a proportion of the water depleted during the day. This buffering effect probably delayed the onset of water stress in *Marrubium* seedlings, increasing seedling survival and growth under the nurse shrub engaged in HL compared to gaps (Brooks et al. 2002, Meinzer et al. 2004).

Our hypothesis that HL would have a positive effect on seedling survival and growth held only in part. We found highest seedling survival in treatments with reduced or prevented competition irrespective of whether HL was present or absent (Net and PVC tubes, respectively) and lowest under full competition, despite HL (Mesh tube). This suggests that the intensity of competition for water between *Marrubium* seedlings and neighbouring plants (*Retama* and understory herbaceous species included) outweighed the positive effects of HL. Plants in PVC tubes did not suffer from competition but did not benefit from HL either, whereas plants in the Net treatment suffered from reduced competition and benefited from HL. Under full competition (Mesh tubes), however, HL did not cancel out consequences of competition and seedlings had lowest survival than seedlings in PVC and Net tubes.

Different results were found for seedling size. Seedlings grew the most under no competition and no HL conditions (i.e., in PVC tubes) and least under full competition and HL (i.e., Mesh tubes), being Net tubes (reduced competition and HL) in between. This shows that belowground competition under *Retama* was more intense than the effects of hydraulic lift. Intermediate seedling size in Net tubes (no roots + water flow) could reflect an intermediate competition level between PVC (no roots, no water flow) and Mesh tubes (roots + water flow), where the role of hydraulic lift seems inconclusive. However, survival rate was similar in Net and PVC tubes, evidencing that HL counterbalanced competition in Net tubes. Overall, our data show that HL played a role in increasing seedling survival although it did not affect seedling size.

Similar effects on plant mass were observed by Ludwig et al. (2004) on grasses growing under lifter *Acacia tortilis* trees when, similarly to our PVC treatment, belowground competition and hydraulically lifted water were excluded. Their results suggested that competition for soil water between tree and understory species was intense and overwhelmed the facilitative effects of hydraulic lift. Hirota et al. (2004) also observed intense competition between rice plants (*Oryza sativa)* and a tree (*Markhamia lutea*) when growing together, but in the long-term rice plants that had access to hydraulically lifted water by the tree remained green whereas rice growing alone died.

Overall, our data show that the extra water provided by *Retama* through HL did not fully compensate for belowground competition in the understory, although it had a significant effect on survival when competition was reduced. We should point out that despite intense belowground competition under *Retama* shrubs, the overall effect of the shrub on seedling survival and growth was positive compared to seedlings in gaps and HL likely played a role in this effect by buffering soil moisture decline in treatments where HL occurred along with belowground competition (Net and Mesh). We do not know, however, whether these effects would be of relevance for adult plants. Previous work reported positive effects of hydraulic lift on the physiology of adult perennial understory species (Dawson 1993, Zou et al. 2005); however, these studies did not analyze the influence of HL on seedlings.

To our knowledge, this is the first study that analyzed the relative importance of HL on seedling survival under a nurse species engaged in HL, teasing out its effects from belowground competition processes in the understory. Separating HL effects from competition effects in the field is not possible though. If lifted water is allowed inside tubes (Net and Mesh), then some water may also leave the tubes in response to neighbours' uptake through passive diffusion not fully isolating the effect of HL. Given these difficulties, we achieved to create a less interactive treatment where competition for water was reduced as much as possible by preventing foreign root growth inside the tubes. This treatment thus allowed us to compare the effects of HL on a gradient from no competition (PVC) to reduced (Mesh) and full (Net) competition allowed. Treatments that allowed flux of hydraulically lifted water to seedling roots (Net and Mesh tubes) were effective since we detected hydraulic lift cycles in psychrometers installed in these treatment tubes. Several studies have demonstrated that neighbours take up the hydraulically lifted water released to their rooting medium (Dawson 1993, Emerman and Dawson 1996, Filella and Peñuelas 2003, Ludwig et al. 2003, Hawkins et al. 2009). Besides, plants probably cannot discriminate between hydraulically lifted water from superficial soil water when taking up water. Hence, it is clear that *Marrubium* seedlings took up hydraulically lifted water by *Retama* nurses in treatments where hydraulic lift took place, but not in PVC tubes where the flux of hydraulically lifted water was prevented.

In summary, we have shown that belowground competition outweighed the positive effects of HL in the understory of *Retama sphaerocarpa* shrubs although HL contributed to seedling survival during summer but not to seedling growth. Both hydraulic lift and belowground competition took place simultaneously although, overall, nurse plants had a net positive effect on survival and growth of seedlings through other mechanisms besides the supplemental water provided via HL and despite the belowground competition for water. The combined effect of microclimate amelioration and improved soil resources under the canopy of *Retama,* with contribution of HL, seems to have outweighed the negative effects of belowground competition.

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Capitulo V

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*Implicaciones de la redistribución hidráulica a nivel de planta y ecosistema**

*Enviado como: Prieto I, Pugnaire FI (2010) Hydraulic redistribution: recent insights on its consequences at the plant and ecosystem level

HYDRAULIC REDISTRIBUTION: RECENT INSIGHTS ON ITS CONSEQUENCES AT THE PLANT AND ECOSYSTEM LEVEL

Summary

Hydraulic redistribution (HR) is the passive phenomenon of water movement between disparate parts of the soil via plant root systems, driven by water potential gradients within the soil. Although the phenomenon has been known for over twenty years, it has received an increased attention in the last decade and our knowledge in this field has increased dramatically. In this review we discuss the main factors controlling HR and the implications for the plant engaged in HR and for plant community and ecosystem processes. Plants benefit from the water provided through HR in several ways and at various levels, positively affecting root growth and functionality, nutrient absorption or plant growth and carbon gain. Neighboring plants can also benefit from the extra water provided via hydraulic redistribution, although the outcome of the interaction mediated through this extra water is species-specific and context dependent. Recent evidence shows that hydraulic redistribution may have important implications at community scale affecting net primary productivity and water dynamics. Globally, hydraulic redistribution might affect the climate and hydrological and biogeochemical cycles.

Introduction

Plant water relations are a key aspect in understanding the ecology of terrestrial plants and one important aspect that determines plant water balance is the process of hydraulic redistribution (Caldwell et al. 1998). The term refers to the passive movement of water through plant roots from moist to dry soil layers, a phenomenon that improves plant water relations, and other related processes, through provision of water to dry soil layers and redistribution of soil moisture within the root system. Research in the field of hydraulic redistribution in the past ten years has been characterised by a mainstream of studies trying to identify the mechanisms of this passive water movement out of the roots and its potential benefits for the belowground plant parts (i.e., root functioning or root xylem cavitation) (Bauerle et al. 2008; Domec et al. 2004), including the movement of water through mycorrhizal fungi associated to plant roots (Querejeta et al. 2003) or its effects on soil nutrient availability to plants, organic matter decomposition and nutrient cycling (Aanderud and Richards 2009). This increased attention to the phenomenon in the last few years has also shed new insights on pre-existing knowledge of the implications of hydraulic redistribution on soil water balance and its temporal and spatial distribution with a number of papers that have described its physiological and ecological implications at the plant, community and ecosystem level.

In this paper, our aim is to review recent literature on hydraulic redistribution from both a physiological and ecological perspective and at an incrementing scale, from the biotic and abiotic mechanisms behind the process, to the link between hydraulic redistribution and plant belowground processes, including its potential effects on biogeochemical cycles as well as to discuss some of its main implications at the individual plant and community level. Increasing evidence derived from implemented models points out that hydraulic redistribution has implications at a regional and global scale including effects on primary productivity (Domec et al. 2010) and water exchange between plant communities and the atmosphere (Lee et al. 2005), all of which will also be discussed in this review.

Main mechanisms controlling the phenomenon of HR

Water efflux out of the roots under specific conditions has been demonstrated in greenhouse experiments in the 1930s (see Ryel et al. 2004 for a historical perspective) but it was not until 1987 that Richards and Caldwell (1987) coined the term "hydraulic lift" to describe the daily patterns observed in soil water potential in dry soil layers under *Artemisia tridentata* shrubs. Soil water potential under the shrubs decreased during the day and increased at night indicating water efflux from roots (Fig 1). When the shrubs were bagged with dark fabric simulating a nighttime period, soil water potential increased continuously until the bags were removed, indicating that hydraulic lift ocurred when stomata were partially closed. Burgess et al. (1998) later used the term 'hydraulic redistribution' to include other direction of water movement through the soil-root continuum; water can move downwards from wet shallow to dry deep soil layers after rain moistens upper soil layers and even laterally from wetter to drier parts of the shallow root system (Smart et al. 2005). Many factors influence the frequency and magnitude of hydraulic redistribution in terrestrial systems; plant traits (e.g., root structure and function, root morphology), plant physiology (e.g., nocturnal transpiration, plant water potential, photosynthetic pathway), soil environment (water potential gradients, soil texture) or climate (rainfall, air humidity).

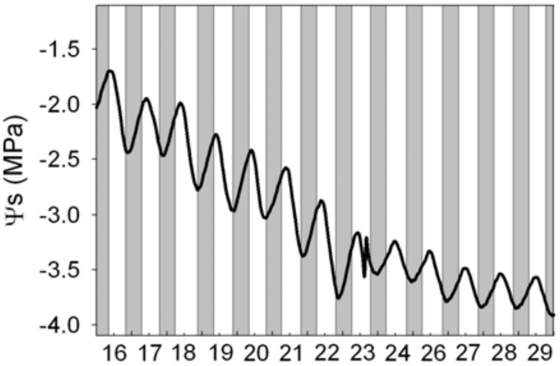

Fig 1. Daily patterns of water flow through the root system under *Salsola oppositifolia* shrubs at 30 cm depicting typical HL cycles. During the day, water flows from the soil up into the atmosphere following the transpiration stream decreasing soil water potential (clear bars). At night, water moves from deep into the shallow soil layers within the root system and is exuded in shallow layers increasing soil water potential (grey bars). When shallow roots were trenched on day 23 the daily cycles were reduced (Prieto et al. unpublished data)

This water movement through plant roots is passive and mainly driven by soil water potential gradients between soil layers with different moisture provided an intact root pathway connects these layers (Leffler et al. 2005). During the day, water is being drawn from the soil as plant transpiration forces the water to flow from the soil, into the roots and out to the atmosphere.

During periods of low vapour pressure deficit (VPD), when stomata in the plant are partially closed and transpiration is lowered or suppressed, plant water potential equilibrates with that of the wettest soil. Thus, water potential of roots in dry soils gets higher (less dry) compared to the surrounding dry soil, and hence, water flows out of the roots and is exuded into dry soil layers, i.e. soils with lower water potential than roots. This water movement usually takes place at night in most plant taxa when stomata are partially closed but occurs during the day in plants with crasulacean acid metabolism (CAM) as they close their stomata during the day (Yoder and Nowak 1999). Partial stomatal closure during daytime has also been reported is some plant species under high VPD conditions during afternoon periods when radiation is high. Under such conditions, hydraulic redistribution can also take place (Espeleta et al. 2004). It is widely assumed that roots connecting both layers act as mere conduits for water movement and that the process is passive and it does not involve a metabolic cost to the plant. The process seems to be ubiquitous (Caldwell et al. 1998), as long as the conditions favour its occurrence, and in only very few of this cases hydraulic redistribution was not detected (Grigg et al. 2009; Scholz et al. 2008). In the '*Belowground processes affected by HR'* section we will discuss some of the main mechanisms that affect its frequency and magnitude in terrestrial systems.

Competing sinks for hydraulically redistributed water (HRW)

It was previously thought that the soil water potential gradient existing between different soil layers was the main driver of hydraulic redistribution (Richards & Caldwell 1987). This is true since the process is effectively inhibited, or changes direction, when dry soil layers are moistened above that of wet layers (Hultine et al. 2004). However, recent evidence has shown that a complex source-sink system is established within the plant as well as between the plant and the surrounding soil changing hydraulic redistribution patterns and magnitude. Water moves within this source-sink system following water potential gradients that depend on soil conditions, plant physiological status and environmental conditions (i.e., soil moisture, plant water status, vapor pressure deficit) (Scholz et al. 2002). Through different manipulations that included lowering leaf water potentials by bagging the plants at night, Scholz et al. (2002) detected that the water movement within plant roots was linearly related to the difference between soil and leaf water potential (Ψ_{leaf}). The same phenomenon was later observed in decidous trees in a neotropical savanna where reverse sap flow in shallow roots – i.e. HR- increased as the difference between root water potential (Ψ_r) and Ψ_s increased (Scholz et al. 2008). These data suggests that the aboveground plant part may act as a competing sink for soil water during nighttime periods reducing the amount of root water efflux in dry soil.

More recently, Hao et al. (2009) observed than in some ecosystems such as in mangles in tropical Florida, the interstitial soil osmotic potential (Ψ_o) component could determine the rate and direction of water movement within the root system independently of the soil matric potential (both osmotic and matric potentials are components of the soil water potential). They observed patterns consistent with hydraulic redistribution in dwarf mangle trees (*Rhizophora mangle*) that had roots connecting a shallow layer with higher salt concentration (greater Ψ_o) and deep layers with a lower salt concentration (lower Ψ_o). Although the matric water potential was similar in both layers, water moved upwards following the osmotic potential gradient from lower to higher Ψ_o. As roots of mangle trees are effective in excluding salts during water uptake, the authors hypothesized that the freshwater movement upwards should help dilute the high salinity in shallow layers and allow dwarf mangle trees to avoid the harm caused by high salt concentrations in the soil.

A common case of a competitive sink for hydraulically redistributed water is nighttime transpiration. In some ecosystems, nighttime transpiration is not uncommon and a great number of species that have been reported to hydraulically redistribute water exhibit this phenomenon (Dawson et al. 2007). During periods of nocturnal transpiration, the aboveground plant parts can act as a competitive sink for soil water that would then move through the roots to the leaves and to the atmosphere. Under these conditions the magnitude of hydraulic redistribution could be reduced). Negative relationships between nighttime sap flow in stems towards the atmosphere and the magnitude of hydraulic redistribution have been widely reported in the literature (Hultine et al. 2004; Prieto et al. 2010a). However, in these studies it was difficult to assess whether nighttime flow in the stem was due to nighttime transpiration or stem tissue water recharge. Whatever the case, the competing sink for HRW being the atmosphere or plant tissue water recharge , the amount of water released into dry soil layers was reduced. Hultine et al. (2003) found that reverse sap flow in shallow roots of *Fraxinus angustifolia* decreased substantially with increasing VPD measured at night. In a more recent study, Howard et al. (2010) demonstrated that nightitme transpiration driven by high VPD conditions can effectively decrease the magnitude of hydraulic redistribution by 73% to 33% in *Artemisia tridentata* and *Heliantus anomalus,* a substantial reduction that could reduce total carbon gain by reducing next day plant transpiration rates (Ryel et al. 2002).

Root function, size and morphology

Besides soil water potential gradients or nighttime transpiration controlling hydraulic redistribution process, the bidirectional movement of water into and out of the roots also implies that roots do not have rectifier properties and that water can move freely in both directions (Caldwell et al. 1998). In the short term, it appears that roots do not exhibit rectifier properties that would preclude water flow out of the roots and thus hydraulic redistribution. A more detailed discussion on this issue is given in detail in Caldwell (1998). However, recent studies have demonstrated that some root properties might indeed affect reverse water flow out of the roots (Dawson 1997, Valenzuela-Estrada 2009, Shulte 2006)

In a greenhouse study with *Accer saccharum* seedlings, Dawson (1997) observed that, under a given pressure, water flow both into and out of the roots was similar for the lowest order roots (fine), but in roots greater than 1.5 mm section diameter, water flow was slightly lower when flowing outside the roots than in the opposite direction. High hydraulic resistance to water flow might also occur in lowest root orders (more distal roots) that would act as a "hydraulic fuse" preventing hydraulic failure of highest root orders (Valenzuela-Estrada et al. 2009), as proposed by Jackson et al. (2000). Evidence of a differential water flow through roots was also observed in Douglas-fir (*Pseudotsuga meinziesii*) trees (Schulte 2006). Water movement through root junctions was restricted in the reverse direction and resistance to water flow was greater when flowing away from the stem and out of the roots than in the opposite direction (towards the stem) (Schulte 2006). Increased resistance to water flow outside the roots might reduce the amount of water that can be redistributed by a plant within a single night.

In the longer term, root xylem cavitation results in loss of root hydraulic conductivity and negatively affects the amount of water that can be lost by the roots, although root xylem caviation would also affect root water uptake from the soil (Domec et al. 2004). In two mature forests, the seasonal loss of shallow root hydraulic conductivity in response to drought was inversely correlated to rates of reverse sap flow in shallow roots (Scholz et al. 2008; Warren et al. 2007) indicating a direct relationship between water transport out of the roots and their hydraulic conductivity.

Other root traits determining the belowground structure of the root system, i.e., root morphology, life history traits or fine root demography are also important attributes determining the occurrence of hydraulic redistribution. In a study carried out in a Brazilian savanna, species with different root system morphology showed distinct hydraulic redistribution patterns (Scholz et al. 2008). Decidous species with dimorphic root systems spanned different soil layers with lateral roots in surface soil and one, or more, taproots accessing deep wet layers. In these species reverse water flow in shallow lateral roots was detected. In contrast, perennial monomorphic species had one or more taproots and lacked true lateral roots in shallow soil and thus did not exhibit reverse flow patterns (Scholz et al. 2008). Similar results were observed in *Acacia ancistrocarpa* trees growing in a north-western Australia desert ecosystem where no reverse flow patterns from primary sinker roots to lateral roots were observed after a simulated 80 mm rain event took place (Grigg et al. 2009). The authors hypothesized that downward water flow might have occurred through secondary sinker roots instead.

Since most water flow occurs in the fine roots (Caldwell et al. 1998), fine root loss or death could lower, or even cease, the magnitude of hydraulic redistribution. Fine root death might occur under some conditions (i.e., low soil water potentials), however, the threshold water potential under which fine root loss occurs is species-specific and varies greatly among species. Hydraulic redistribution has been shown to cease at soil water potentials that range from as high as -1.5 MPa (close to the wilting point for most herbaceous species) to as low as -8.5 MPa (Meinzer et al. 2004; Prieto et al. 2010a). Querejeta et al. (2003) found water movement could occur through the mycelium net of mycorrhizal fungi connected to fine roots when soil water potential was as low as -20 MPa. Fine root density and differential root colonization can also affect hydraulic redistribution patterns. In patches where root density is high, soil water is depleted at a faster rate as more water is being drawn from the soil, thus creating a heterogeneity of water potential gradients within the root system and a preferential flow of HRW to this soil patches (Warren et al. 2007; Xu et al. 2007). This results in a patchy hydraulic redistribution pattern and different water efflux rates within the root system.

Soil texture

Soil texture determines the amount of water that a soil can retain as well as the amount of water that can be extracted by plant roots at different soil water contents (Hultine et al. 2004). In a similar way, soil texture affects the amount of water that can be released through plant roots. The first evidence came from a field study in the Mojave Desert, where Yoder and Nowak (1999) observed that the magnitude of hydraulic redistribution decreased with increasing sand content in the soil (measured as a percentage of coarse texture fraction). They concluded that coarse textured soils were less conducive for hydraulic redistribution than finer textured soils. Greater increases in soil water potential overnight were also detected under *Sarcobatus vermiculatus* individuals growing in soils with 92% sand fraction than in *A.tridentata* shrubs growing in loamy sand soils with 75% sand fraction (Aanderud and Richards 2009). However, these differences might have been due to differential species-specific capacity to perform hydraulic redistribution or different soil water potential gradients between soil layers. Cotton plants that grew in clayey soils also showed greater increases in soil water content overnight, and hydraulic redistribution cycles were detected for a longer period than in plants growing in sandy soils (Wang et al. 2009). Recently, using a simple modelling approach and the Van Genuchten (1980) parameters in a range of different textures, Prieto et al. (2010b) observed the relationship between hydraulic redistribution and soil texture was non-linear. Fine textured soils were more conducive to hydraulic redistribution than coarse textured soils, with intermediate textured soils (loamy soils) being the most conducive of all soil types. Very fine-textured soils (i.e, clayey soils) seemed to have intermediate properties between them, which could result in context-dependent hydraulic redistribution patterns.

Belowground processes affected by HR

Benefits to roots

It has been previously discussed how several root attributes influence the magnitude, frequency and duration of hydraulic redistribution, but: How do roots benefit from HR? Caldwell et al. (1998) proposed that several benefits to plant roots could arise from the release of soil moisture in dry soil layers. They hypothesized that a reduction of soil drying through hydraulic redistribution would prolong survival and growth of fine roots developing in dry soil. Bauerle et al. (2008) tested this hypothesis in a field experiment using two *Vitis sp*. cultivars that were irrigated only in one side of their root system and where hydraulic redistribution was prevented with nighttime illumination in half of the plants. They monitored root water potential and fine root survival in the dry part and observed that water potentials were twice as negative in roots growing under dry soil than in those were HR occurred. Those plants where hydraulic redistribution was circumvented reduced root survivorship by 50% in the dry soil root portion compared to plants that benefited form HRW. Rehydration of fine root tissues through internal hydraulic redistribution was responsible for this effect. This might have great implications in plant carbon budgets, plant water absorption and nutrient uptake since roots live longer and can absorb water and nutrients for a prolonged time and do not need to be replaced at a carbon cost to the plant.

In general, plant roots have longer vessels and are more vulnerable to cavitation and hydraulic failure than stems and they also have narrower safety margins (Martínez-Vilalta et al. 2002). Carbon costs associated with building new roots are usually lower for roots than for branches or stems (Hacke et al. 2000). Hence, avoiding root water potentials to drop below their threshold value before hydraulic failure occurs might be crucial for terrestrial plants to cope with drought periods in drought prone ecosystems. Through provision of overnight HRW to drier parts of the root system, hydraulic redistribution helps maintain root conductivity and prevents roots from reaching water potentials below their hydraulic failure threshold, avoiding loss of root water transport (Domec et al. 2004). Besides the direct benefit for root survival and function already discussed, redistribution of water within the root system helps equilibrate the whole plant water potential with the surrounding soil overnight, likely diminishing the water stress experienced by the plant during the next day (Ryel et al. 2003). Through the refilling of xylem vessels overnight, root xylem embolism could be recovered as much as 55% the next morning (Domec et al. 2006). Domec et al. (2006) showed that water provided through hydraulic redistribution was sufficient to maintain root hydraulic conductivities at levels above their threshold water potentials that prevented complete root rectification and complete loss of water transport. In terrestrial plants, loss of root conductivity negatively affects root water transport capacity and leaf stomatal conductance and thus, the recovery of root conductivity overnight may help maintain greater stomatal conductance the next day and in turn, greater overall plant carbon gains (Domec et al. 2006).

Influence of HR on nutrient capture and decomposition processes: the role of mycorrhizal fungi

In the soil matrix, nutrients are found in both a solid phase and in soil solution. Microbial activity in the soil decomposes the organic matter (mainly litter) and mineral compounds releasing nutrients as ions that incorporate into the soil solution. These ions need to be transported close to the roots for absorption and this movement occurs through two main pathways, via mass flow driven by transpiration fluxes or via diffusion. All of the aforementioned processes are highly dependent on soil moisture conditions (Nye & Tinker 1977). Water efflux into the soil surrounding the vicinity of the roots overnight can maintain high soil moisture conditions for several weeks and increase the availability of water in shallow layers, both spatially and temporally, maintaining nutrients available for plant absorption for a longer period (Meinzer et al. 2004; Ryel et al. 2002; Siqueira et al. 2008). Matzner & Richards (1996) proposed that the observed ability of *Artemisia tridentata* shrubs to maintain nutrient uptake under very dry soil conditions (< -5 MPa) was enhanced by the release of water through hydraulic redistribution but they did not directly tested it. Dawson (1997) grew *Accer saccharum* seedlings and suppressed water efflux from roots in half of the seedlings through constant illumination at night whereas the other half was allowed to hydraulically redistribute water. With this experimental design, he demonstrated that nutrient availability (N, P, K) increased around roots of plants performing hydraulic redistribution with nitrogen being most affected. However, he did not test the direct effects of this greater availability on nutrient plant absorption. Other authors observed evidence of greater plant nutrient uptake from dry soils aided by hydraulic redistribution processes in different shrub and grass species but it was difficult for the authors to differentiate whether nutrient uptake was directly linked to the efflux of water or to other side effects, for example greater overall water availability (de Kroon et al. 1998; Huang 1999; Leffler et al. 2004; Valizadeh et al. 2003). By experimentally manipulating nighttime transpiration, Snyder et al. (2008) observed a tendency of greater N uptake in semi-arid *Sarcobatus vermiculatus* shrubs with suppressed nighttime transpiration (and thus greater HR) than plants that were left un-bagged but results were only marginally significant (*P* = 0.07) suggesting a direct role of hydraulic redistribution on nutrient uptake.

Recent evidence in this field points out in this direction. Hydraulic redistribution through plant roots effectively enhances mineralization rates and decomposition of the organic matter contained in the soil releasing nutrients that would later be absorbed by the plant (Aanderud & Richards 2009, Armas et al. unpublished). Aanderud & Richards (2009) studied decomposition rates under two semi-arid shrub species (*Artemisia tridentata* and *Sarcobatus vermiculatus*). They found that decomposition rates were 25 % greater under *A. tridentata* in dense root patches than in sparse roots patches. Although soil water potential was lower in the dense root treatment, the increase in decomposition rates correlated to the three-fold greater hydraulic redistribution magnitude observed in the root dense treatment. Armas et al (unpublished) found similar results in semi-arid Buffalograss plants (*Buchloe dactyloides*). Enhanced soil moisture and the daily drying-rewetting cycle of hydraulic redistribution might create a daily rhythm of root water fluxes and rhizodeposition that increases microbial activity and decomposition rates (Cardon and Gage 2006). Under Buffalograss (*Buchloe dactyloides*) plants that performed hydraulic redistribution mineralization rates were also greater after more than two months of drought (Armas et al. unpublished). Bufalograss plants that performed hydraulic redistribution also took up greater amounts of labelled ^{15}N that was previously added to the soil as dry organic matter. In a similar study with the semi-arid shrub *Retama sphaerocarpa*, Prieto et al. (unpublished) observed greater ^{15}N uptake from nutrient rich soil patches (dry organic matter) in shrubs that performed hydraulic redistribution. Cladode ^{15}N concentration was directly correlated to the amount of water released into dry soil indicating enhanced water availability was responsible for the nutrient uptake. An interesting result from this study was that hydraulic redistribution enhanced root foraging, or the growth of roots in nutrient rich patches, suggesting that hydraulic redistribution might play a direct role in root foraging strategies.

In association with mycorrhizal fungi (MF), plants can improve their water status through improved nutrient uptake, especially phosphorus and nitrogen (Allen 2003). Hydraulically redistributed water can move out of the roots and into the soil via mycorrhizal fungi associated to plant roots (Querejeta 2003) and this water source allows MF to remain active at water potentials as low as -20MPa. Thus, hydraulic redistribution via MF could indirectly enhance nutrient uptake in very dry soils, prolonging the period of nutrient uptake by the plant. Egerton-Warburton (2008) tested this hypothesis in *Quercus agrifolia* seedlings growing in chambers with two compartments placed horizontally and separated by a fine mesh that excluded roots but allowed mycorrhizal fungi to grow through. They found that water efflux into the soil in the fungal compartment was correlated to labelled ^{15}N uptake by *Quercus* seedlings and that water efflux was also correlated to soil bacterial abundance and enzymatic activity, suggesting that hydraulic redistribution through the extramatrical hyphal mycelia enhanced both plant nutrient uptake and soil microbial processes. The direct role of hydraulic redistribution on plant nutrient uptake, however, was not clear, as water influx was also correlated to nutrient uptake by *Quercus* seedlings. These authors proposed two alternative mechanisms by which hydraulic redistribution might influence nutrient capture by plants. An indirect mechanism mediated by increased soil water availability that enhances microbial and enzymatic activity and a direct role of extramatrical hyphae maintaining nutrient uptake since HR tends to increase their functionality in dry soils (Lilleskov et al. 2009; Querejeta et al. 2003; Querejeta et al. 2007).

Ecological implications

We have discussed in previous sections the importance of root water efflux on several aspects of the plant physiology and the main findings in the field of hydraulic redistribution. Nonetheless, the quantitative importance of hydraulic redistribution for ecosystem structure and function are still unclear (Katul and Siqueira 2010). The improvement and use of recent techniques such as sap flow or Eddy covariance have improved our knowledge in this field and modelling efforts are increasingly shedding light on the ecological importance of hydraulic redistribution at a global scale.

Hydraulic redistribution mediates plant-plant interactions

Water parasitism has been widely documented in the literature (Caldwell 1990; Dawson 1993; Filella and Peñuelas 2003). This term refers to the capacity of understory species that grow next to a species engaged in hydraulic redistribution to be able to take up the water that is lifted to shallow layers at night (Caldwell 1990). The first evidence of uptake of HRW by neighbouring species was obtained by Caldwell and Richards (1989) when they observed that the isotopic signature of water extracted from deep layers and released in upper soil layers by *Artemisia tridentata* shrubs was the same as in neighbouring *Agropyron desertorum* stem water. However, in a consequent study with the same species, transpiration rates did not decrease in *A.desertorum* grasses when hydraulic redistribution was curtailed in neighbouring *Artemsia* shrubs (Caldwell 1990). Since then, evidences of water parasitism by neighbouring species have been found in several ecosystems and plant species with different life forms (Table 1). There are two possible pathways by which plants can acquire HRW from a neighbouring plant engaged in hydraulic redistribution; i) directly through the soil after the release of HRW by shallow roots or ii) directly through common mycorrhizal fungi hyphal networks (CMN) linking different individuals within a community (Egerton-Warburton et al. 2007; Warren et al. 2008). Apparently, the last pathway seems to be the most efficient, as water is transported directly between donor and receiver species via CMN but the relative importance of each pathway still remains uncertain (Schoonmaker et al. 2007).

Deep-rooted plants lose water to the soil in upper layers overnight but also take up water and nutrients during the day. Thus, they compete for soil water with neighbouring species and the net effect that these species have on their neighbours is not certain. Most studies in this field have reported net effects that range from positive, to neutral or even negative depending on the type of ecosystem, the plant life forms involved in the interaction or whether donor or receiver species share CMN (Table 1). Ludwig et al. (2004) reported an intense competition for water between *Acacia tortilis* and three grass species that grew in its understory. Although the grasses in contact with *A. tortilis* roots were able to effectively take up the water redistributed from deep layers, their biomass was lower than in grasses growing where roots of the tree were experimentally removed. Other studies using grass species growing in close proximity to trees that were engaged in hydraulic redistribution have reported similar results (Table 1). Nevertheless, positive effects on grasses have been also reported (Dawson 1993). On the other hand, plant interaction studies that have used shrub species in association with a tree or shrub engaged in hydraulic redistribution have reported either positive or neutral effects (Table 1). Zou et al. (2005) observed a differential effect of HRW on different shrub species growing under *Prosopis glandulosa* trees concluding that the effect of hydraulic redistribution on neighbouring species might be species-specific.

Grass species usually have shallow extensive root systems (Schenk and Jackson 2002) and a great capacity to extract soil water, which makes them great competitors, especially in dry ecosystems where water sources are scarce (Noy-Meir 1973). In association with a species that performs hydraulic redistribution, the amount of water redistributed by the tree might not be enough to meet the requirements of the grass and depletion of water by the nurse species would exert a greater negative effect on the grass than the benefit of the extra water source provided through hydraulic redistribution. In this case, competition would be the predominant net outcome of the interaction (Ludwig et al. 2004). Shrubs, on the other hand, are usually deeper rooted than grasses and have a less extensive root system (Schenk and Jackson 2002)

Table 1. Summary of earlier works analyzing the effects of hydraulic redistribution (HR) on plant-plant interactions in species of similar or different life forms. Results on the facilitative effects of hydraulic redistribution are controversial. Positive or neutral effects are mostly found when target shrub or tree species were used and negative effects have been mostly observed on grass species, with the exception of Dawson 1993. In the latter case, great differentiation between soil layers with a fragipan at 80cm depth and a groundwater table at a shallow depth greatly enhanced the amount of water redistributed, which might not be representative of conditions under which hydraulic redistribution occurs in most ecosystems. δD = deuterium content of xylem water; Ψ_l = leaf water potential; Ψ_{pd} = plant predawn water potential; A = CO_2 exchange in green leaves; g_s = stomatal conductance to water vapour; $\delta^{13}C$ = isotopic carbon content in dry leaves; F_v/F_m = photosynthetic efficiency of photosystem II. Not det = not detected

Sp. engaged in HR	Target species	Growth form	Measured variable	Net effect	Reference
Accer saccharum	*Asarum canadense*	Grass	δD /Growth / Ψ_l/ g_s	+	Dawson 1993
	Fragaria virginiana	Grass		+	
	Podophyllum peltatum	Grass		Not det	
	Solidago flexicaulis	Grass		+	
	Thalictrum dioicum	Grass		+	
	Lindera benzoin	Shrubs		Neutral /+ /+	
	Vaccinium vacíllans	Shrubs		+	
	Acer saccharum	Tree		+	
	Acer negundo	Tree		+	
	Betula Zutea	Tree		+	
	Fagus grandifolia	Tree		Neutral /+ /+	
	Pinus strobus	Tree		+	
	Tilia heterophylla	Tree		Neutral /+ /+	
	Holcus lanatus	Monocot		+	
	Smilacina racemosa	Monocot		Not det	
	Trillium grandifiorum	Monocot		Not det	
Acer saccharum	*Acer saccharum*	Tree	δD / g_s	+	Dawson 1996
Pinus halepensis	*Pistacia lentiscus*	Shrub	δD / $\delta^{13}C$ / Ψ_{pd}	+	Filella & Peñuelas 2003
Acacia tortilis	*Cynodon dactylon*	Grass	Biomass (g)	—	Ludwig et al. 2004
	Panicum maximum	Grass		—	
	Cenchrus ciliaris	Grass		—	
Cajanus cajan	*Zea mays*	Grass	δD	Not det	Sekiya & Yano 2004

Table 1. (*Continued*)

Sp. engaged in HR	Target species	Growth form	Measured variable	Net effect	Reference
Markhamia lutea	*Oryza sativa*	Grass	g_s	—	Hirota et al. 2004
Prosopis velutina	*Zanthoxylum fagara*	Shrub	Ψ_l / A	+	Zou et al. 2005
	Berberis trifoliolata	Shrub		Neutral	
	Condalia hookeri	Shrub		—	
Pseudotsuga menziesii	*Berberis nervosa*	Shrub	δD	Not det	Brooks et al. 2006
	Tsuga heterophylla	Tree			
	Vaccinium spp	Shrub			
	Gaultheria shallon	Shrub			
Pseudotsuga meinziesii	*Pseudotsuga meinziesii*	Tree	δD / Biomass / Ψ_{pd}	Neutral	Schooonmaker et al. 2007
Pinus ponderosa	*Festuca pallescens*	Grass	δD / Growth	—	Fernández et al. 2008
Protea (Sylvia)	*Leysera gnaphalodes*	Shrub	δD	+	Hawkins et al. 2009
	Cyanodon dactylon	grass			
Pistacia lentiscus	*Juniperus phoenicia*	Shrub	δD / Ψ_{pd} / g_s / δ^{13}C / A / RWC / (F_v /F_m)	—	Armas et al. 2010
Retama sphaerocarpa	*Marrubium vulgare*	Shrub	Survival / Biomass	+	Prieto et al. Unpublished

gaining access to deeper water sources and becoming less dependent of water extraction from shallow layers. In this case, depletion of water by the tree engaged in hydraulic redistribution in shallower soil layers might exert a smaller effect on the performance of the neighbour shrub whereas the latter can benefit of small water additions into the soil. Dawson (1993) observed that there was a strong linear relationship between the benefits obtained in terms of growth and the proportion of HRW taken up by different understory species. Indeed, although individuals belonging to both life forms (grasses and shrubs) benefited from the presence of the tree, herbaceous species took up on average a greater proportion of HRW than did shrubs.

Another interesting question that arises from the role of hydraulic redistribution on the interaction between higher plant species is whether water parasitism is such or, on the other hand, the species engaged in hydraulic redistribution also benefits from the association at the cost of loosing a portion of the redistributed water. A piece of evidence comes from a case study in southeast Spain where Prieto et al. (unpublished) have observed that, although competition for water between the nurse shrub *Retama sphaerocarpa* and seedlings of the neighbouring shrub *Marrubium vulgare* was strong, *Retama* facilitated survival of *Marrubium* seedlings under its canopy and that, among others, one of the mechanisms involved in this facilitation was hydraulic redistribution. In this particular case, *Retama* also benefits indirectly from the association with *Marrubium* through improved nutrient uptake and water relations (Pugnaire et al. 1996). Thus, it could be that loosing some of the redistributed water transported to upper soil layers at night might report an indirect benefit of an association with a species that depends on this HRW for survival during drought periods. However, evidence comes from a single study and further research in the field of plant facilitation and the role of HRW on plant-plant interactions.

Biogeochemical implications

The mobilization of nutrients or mineral elements from different pools in the soil might have broad effects at an ecosystem scale in the bioengineering of soils (Verboom and Pate 2006). The implications of hydraulic redistribution in translocation of nutrients and soil formation are clearly illustrated in the clay neo-formation process observed under mallee eucalypts (*Eucaliptus incrassata, E. pleurocarpa, E. Decipiens and E. Occidentalis*) growing in a sand dune system in Australia (Verboom and Pate 2010). The deposition of metals (Al, Si and Fe) associated to clay formation in the upper portion of the dunes was transported from deep soil layers via hydraulic lift and played a pivotal role in pavement construction around eucalyptus roots.

The downward movement of water through hydraulic redistribution could also help mobilize deep nutrient pools (Rumpel and Kögel-Knabner 2010; Walvoord et al. 2003) and allow nutrients to be transported upwards to shallow layers by a mechanism known as “nutrient uplift” (Jobbagy and Jackson 2004). In most systems nutrients are stored in the upper shallow layers but in some arid and semi-arid ecosystems a large storage of nitrate (NO_3^{-2}) was reported in deep layers (Walvoord et al. 2003) although there is some uncertainty that this is a global trend (Jackson et al. 2004). McCulley et al (2004) suggested that the efflux of water transported through hydraulic redistribution to deep soil layers might increase nutrient uptake by deep roots and the incorporation into plant tissues may help increase the rate of "nutrient uplift" to shallow layers (Matzner and Richards, 1996, Jobbagy and Jackson, 2004).

Although it is clear that plant roots can take up and exude water into the soil at similar rates depending on water potential gradients, the release of ions or other metal compounds to the soil aided by hydraulic redistribution processes remains unclear. Water-soluble compounds like some small ions (K^+, Na^+ or Cl^-) that can diffuse via mass flow into roots can be directly transported diluted in root sap. Recent evidence obtained in a sand dune system in semi-arid southeast Spain over salty groundwater suggests the possibility that some salt-tolerant species might redistribute salt ions to upper soil layers through hydraulic redistribution (Armas et al. 2010). In this study, deep-rooted and salt-tolerant *Pistacia lentiscus* exerted a negative effect on the performance of salt intolerant *Juniperus phoenicia*. This negative effect was attributed to the release of salty HRW into shallow soil layers by *Pistacia* shrubs. Not surprisingly, osmolality of expressed sap values in plant stems was lower in *Juniperus* shrubs growing alone than when they grew in close association with *Pistacia* shrubs during the dry season when hydraulic redistribution took place. This hypothesis remains to be tested but the scarce evidence in this field points in the direction that not only water is redistributed by plant roots but other compounds like metals or water-soluble ions could be redistributed as well, with potential consequences on the biogeochemical cycles of some important nutrient elements and on plant-plant interactions.

Effects at an ecosystem scale

Globally, plant roots are most dense in the upper 2 m of soil and deep roots usually represent less than 10% of the total root system in trees and shrubs (Canadell et al. 1996). Hence, soil moisture is usually depleted at a faster rate in upper layers creating a soil water potential gradient between deep and shallow layers that drives hydraulic redistribution. Water redistributed at night to upper soil layers provides a source of soil moisture in shallow layers enhancing plant transpiration rates the next day (Richards & Caldwell 1989). Reported values of transpiration increases due to hydraulic redistribution range from 10-40% water in tropical systems (da Rocha et al. 2004), 20-25% in arid and semi-arid environments (Ryel et al. 2002), 19-40% in mesic forests (Jackson et al. 2000) and up to 81% in Mediterranean ecosystems (Kurz et al. 2006).

But, besides overall benefits to individual plants, what are the main ecological implications of increased transpiration in species that perform HR? Recent techniques used to monitor gas exchange between the plant and the atmosphere (Eddy covariance towers) combined with the measure of several soil and plant physiological parameters (i.e. soil water content, root sap flow, root distribution patterns) and later implementation into global gas-exchange models has proved useful at elucidating the implications of hydraulic redistribution globally. Lee et al. (2005) implemented a soil-vegetation-atmosphere water transfer model that included the phenomenon of hydraulic redistribution. They observed that water transfer between deep and shallow soil layers overnight in an Amazonian forest increased photosynthetic rates and whole-stand summer transpiration by ~ 40%. The cooling effect of increased plant transpiration affected the seasonal cycles of air temperature reducing dry season surface-air temperature by more than 2ºC through a change in the latent heat of the atmosphere. A run of their model for the whole globe estimated a decrease in air temperatures of up to 2ºC in most water-stressed regions, a value that could be underestimated in some water-stressed ecosystems where the process of hydraulic redistribution might account for up to 81% of total tree transpiration during drought (Kurz et al. 2006).

At a regional scale, Domec et al. (2010) implemented a model in a loblolly pine (*Pinus taeda*) forest on a coastal plain in North Carolina and included both hydraulic redistribution processes and nocturnal transpiration. At the same time both soil heterogeneity and transpiration from both herbaceous and woody species were measured. They observed between a 30% and 50% increase in whole ecosystem transpiration with hydraulic redistribution, a value similar to that of Lee et al. (2005) that lead to an overall increase in carbon gain. Annual gross ecosystem productivity (GEP) and net ecosystem exchange (NEE) in this forest increased by 750 and 400 gC m^2 year-^{1} respectively with hydraulic redistribution, and during drought it maintained GEP over ecosystem respiration (ER) maintaining the whole forest as a carbon sink. This property might have important implications for overall ecosystem productivity and CO_2 exchange processes in water limited systems or ecosystems with a marked drought period. Besides these effects, enhanced transpiration rates might also affect the hydrological cycle. In a temperate forest of *Accer sacharum*, water available for runoff was between 3 and 6% lower due to enhanced transpiration rates by hydraulic redistribution influencing the hydrological cycle of a whole watershed and lowering several meters the water table due to increased water consumption from deep layers (Jackson et al. 2000).

The downward movement of water to deep layers (Burgess et al. 1998), when scaled at a regional stand level or a whole ecosystem in a watershed, can also affect the water budget increasing the recharge of water in deep soil layers. Water movement after a rain event is faster through hydraulic redistribution via plant roots than infiltration rates or preferential flow through soil pores and cracks. In such cases, water recharge to deep soil layers would be minimal in the absence of hydraulic redistribution recharge (Ryel et al. 2003). In a tropical rainforest in the Amazon, 10% less water was available for runoff due to enhanced downward hydraulic redistribution during the winter rain period coinciding with a ~10% increase in soil water recharge in deeper soil layers (Lee et al. 2005). The water stored in deep layers via HR can be later used in transpiration processes during the drought period extending the deep-rooted plants' growing season (Ryel et al. 2002; Scott et al. 2008). Between 29 and 49% of the rain water that fell during the winter in a *Prosopis velutina* savanna was banked in deep layers, which accounted for 16-49% of transpiration during the following summer allowing plants to better cope with summer drought (Scott et al. 2008). In arid and semi-arid environments where deep-water recharge through precipitation inputs rarely occurs (Sala et al. 1992), recharge through hydraulic redistribution might account for a great proportion of the water used by the plants during drought. Redistribution of water to deep soil layers might also occur during drought periods after a rain event moistens the soil. The redistribution of water evenly within the root system allows for a more conservative way of using water that would be used at a faster rate otherwise (Ryel et al. 2002). Thus, hydraulic redistribution might be of great importance not only for deep-water recharge during winter but for increasing the efficiency of use of transient rain events during the summer period when evaporation in the soil is highest. Ryel et al. (2003) calculated that 100% of an 8 mm rain event that infiltrated below 30 cm came from hydraulic redistribution in an *Artemisia tridentata* stand. In arid and semi-arid ecosystems, rain events greater than 10 mm are rare during the summer period (less than 20% occurrence) (Loik 2007). In a study carried out in central Utah, plant water potential measured during a summer period in *Artemisia tridentata* shrubs declined below -7 MPa (Prieto and Ryel, unpublished). In the same study, shrubs that received a simulated 20 mm rain event were able to redistribute this water to deeper layers and maintained plant water potentials above those plants that did not receive any rain even after more than 30 days of drought. Our calculations estimated that there was a time lag of approximately 11 days before the shrubs that received the pulse reached the same water potentials as plants that did not. These greater water potentials maintained through a conservative water use can also imply greater stomatal conductance during the day, as plants would experience lower water stress, and increased plant carbon fixation rates which could be used for plant storage, growth or reproduction. Scaled at an ecosystem level, downward hydraulic redistribution might not only help the storage of water during winter but also allow whole plant stands to survive extremely long summer drought periods and persist in time through a conservative way of using small rain events during drought.

Synthesis and conclusions

In this review we found that hydraulic redistribution has been reported in over 60 species worldwide and in several ecosystems, from tropical forests (Oliveira et al. 2005) to temperate forests (Dawson et al. 1993) to arid and semi-arid ecosystems (Ryel et al. 2002; Prieto et al. 2010a, 2010b, Armas et al. 2010,Yoder & Nowak 1999). Its effects both above- and belowground are increasingly well understood. Most of its benefits to individual plants come from increased soil moisture in dry soil layers which in turn affects the physiology of plants that are engaged in hydraulic redistribution and soil processes in their rhizosphere, i.e. nutrient mineralization rates or soil organic matter decomposition, with potential global implications in nutrient cycling.

Plant-plant interactions determine plant community structure and function (Callaway 2007) and, although consequences of hydraulic redistribution for neighbouring species are many and range from negative to positive effects, increasing evidence shows that provision of water through hydraulic redistribution is a facilitation mechanism in many plant communities where recruitment is mostly restricted to the understory. Shared mycorrhizal networks appear to play a big role in water redistribution in some ecosystems although more evidence is needed on the rates and magnitude of water transfer between adult plants.

As proposed (Katul and Siqueira 2010), a different approach has to be taken if global and ecosystem effects of hydraulic redistribution are to be understood. Hydraulic redistribution plays a crucial role in water and energy fluxes in the ecosystem, and in recent years our knowledge on community- and ecosystem-level effects has improved by incorporating hydraulic redistribution processes into hydrological and ecological models. One of the most important aspects is that the phenomenon can increase overall plant transpiration rates by up to 81%, increasing ecosystem productivity and maintaining the ecosystem as carbon sink. The IPCC has predicted a global increase in air temperature and VPD, and more infrequent and bigger rain events in most arid and semi-arid ecosystems. In this global warming context, increased temperature and VPD would ultimately increase water demand by plants, likely leading to the depletion of deep-water reserves that might preclude the occurrence of hydraulic redistribution in some ecosystems (Jackson et al. 2000) therefore reducing the potential buffering effect on surface-air temperatures and C sequestration. However, more research on hydraulic redistribution and its inclusion on hydrological and ecological models are needed to fully elucidate its role in net carbon exchange and gross ecosystem productivity, as well as water budget and water transfer through the soil-plant-atmosphere continuum.

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Conclusiones

Patrones de redistribución hidráulica y su importancia en zonas áridas

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A continuación se enumeran las principales conclusiones obtenidas:

1. *Retama sphaerocarpa* realiza levantamiento hidráulico durante el periodo nocturno, cuando la transpiración de la planta es mínima. El levantamiento hidráulico se detectó en todas las estaciones, siguiendo un patrón estacional dependiente del potencial hídrico del suelo en superficie.

2. Los patrones de levantamiento hidráulico y su magnitud están negativamente relacionados con la transpiración nocturna, siendo la magnitud del levantamiento menor cuando mayor es el flujo de savia nocturno en el tallo.

3. El levantamiento hidráulico depende de la transpiración, ya que el potencial hídrico del suelo aumenta de forma contínua cuando la transpiración es inhibida, lo que puede ser relevante para la planta durante periodos de baja evapotranspiración (días nublados y con bajo déficit de presión de vapor).

4. La aportación de agua por levantamiento hidráulico depende de la textura del suelo, siguiendo una relación no lineal con la textura. El efecto de el levantamiento hidráulico es menor en texturas gruesas (arenas) y mayor en texturas intermedias (limos).

5. La redistribución hidráulica favorece el crecimiento de raíces en parches de suelo ricos en nutrientes, aumentando la descomposición de la materia orgánica y la absorción de nitrógeno por parte de la planta.

6. El arbusto *Retama sphaerocarpa* tiene un marcado efecto nodriza facilitando la supervivencia y creciminento de plántulas de *Marrubium vulgare* debajo de su copa. La redistribución hidráulica es uno de los mecanismos implicados en esta facilitación ya que favorece el asentamiento de las plántulas de *Marrubium*. Sin

embargo, los efectos de la competencia por el agua durante la época de sequía superan a los beneficios debidos al levantamiento hidráulico.

7. La redistribución hidráulica afecta numerosos procesos, entre los que se incluyen la dinámica de comunidades vegetales y los ciclos hidrológicos y biogeoquímicos.

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